UNIVERSITÉ DU QUÉBEC À MONTRÉAL

TOLÉRANCE ET LARGEUR DE NICHE DES ESPÈCES HERBACÉES DES FORÊTS QUÉBÉCOISES VIS-À-VIS DU PH ET DE LA LUMIÈRE

MÉMOIRE
PRÉSENTÉ
COMME EXIGENCE PARTIELLE
DE MAÎTRISE EN BIOLOGIE

PAR
LIONEL HUMBERT

SEPTEMBRE 2006

UNIVERSITÉ DU QUÉBEC À MONTRÉAL
Service des bibliothèques

Avertissement

La diffusion de ce mémoire se fait dans le respect des droits de son auteur, qui a signé le formulaire *Autorisation de reproduire et de diffuser un travail de recherche de cycles supérieurs* (SDU-522 – Rév.01-2006). Cette autorisation stipule que «conformément à l'article 11 du Règlement no 8 des études de cycles supérieurs, [l'auteur] concède à l'Université du Québec à Montréal une licence non exclusive d'utilisation et de publication de la totalité ou d'une partie importante de [son] travail de recherche pour des fins pédagogiques et non commerciales. Plus précisément, [l'auteur] autorise l'Université du Québec à Montréal à reproduire, diffuser, prêter, distribuer ou vendre des copies de [son] travail de recherche à des fins non commerciales sur quelque support que ce soit, y compris l'Internet. Cette licence et cette autorisation n'entraînent pas une renonciation de [la] part [de l'auteur] à [ses] droits moraux ni à [ses] droits de propriété intellectuelle. Sauf entente contraire, [l'auteur] conserve la liberté de diffuser et de commercialiser ou non ce travail dont [il] possède un exemplaire.»

REMERCIEMENTS

Je ne pouvais commencer ce rapport sans dire un grand merci à Christian Messier et Daniel Kneeshaw sans qui rien n'aurait été possible, et qui malgré un emploi du temps chargé m'ont bien encadré. J'aimerais également remercier les membres de leur laboratoire respectif qui m'ont accueilli dans leurs locaux. En particulier Dominique Gravel avec qui les discussions et le partage d'information fut très profitable, Henrik Hartmann pour le bon temps passé au Témiscamingue, et Patrick Carrier et les Romains qui m'ont permis de décompresser. Je n'oublierai pas non plus Daniel Gagnon pour ses conseils, Sophie Gachet et Timothy Work pour les corrections, ainsi que les autres membres du GREFi. Un mot également pour Dominic Sénécal, Julie Poulin, Luc Lauzon, les gardiens de la réserve faunique de Papineau-Labelle et Denis Boileau (MRN de Ville-Marie) qui m'ont aidé dans ce projet. Je remercie également Tembec et le Ministère des ressources naturelles et de la faune pour leur soutien à support. Enfin, un grand merci aux deux réviseurs anonymes qui ont permis d'améliorer le premier chapitre de ce mémoire et à leurs encouragements, ainsi qu'a Monsieur Müller l'éditeur en chef de la revue Ecological Indicators où il est actuellement sous presse : Humbert L., Gagnon D., Kneeshaw D. and Messier C., 2006. A shade tolerance index for common understory species of northeastern North America. Ecological Indicators. In Press, Corrected Proof, Available online 18 January 2006.

TABLE DES MATIÈRES

LISTE DES FIGURES

LISTE DES TABLEAUX

RÉSUMÉ

Ce mémoire se propose de qualifier la tolérance à l'ombre, la tolérance au pH et la plasticité de la végétation herbacée du sous-bois dans le Nord-Est de l'Amérique du Nord, plus particulièrement au Québec. La caractérisation de la végétation herbacée, ainsi que des semis d'arbres, s'est longtemps limitée à une brève description de celle-ci sur le terrain. Peu d'études se sont intéressées à finement établir leurs caractéristiques selon les grands gradients environnementaux. Pour ce qui est de la tolérance à l'ombre, la plupart des études classifient les espèces en trois classes : sciaphiles, photophiles et héliophiles. Ces trois classes regroupent respectivement les espèces liées aux couverts très fermés, les espèces de demi-ombre se retrouvant dans les lisières et les taillis et finalement les espèces de milieux ouverts. Dans ce mémoire, nous avons essayé d'étendre cette classification à neuf classes de tolérance à l'ombre à la manière d'Ellenberg *et al.* (1992). A l'aide de données d'experts et issues de la bibliographie, nous avons caractérisé la tolérance à l'ombre de 347 espèces, dont 71 espèces ligneuses au stade de semis, 185 espèces herbacées et 91 espèces de bryophytes et lichens. Ce qui ressort également est la forte concordance des valeurs obtenues par rapport aux données européennes existantes. Cette similarité est très forte pour les plantes invasculaires (bryophytes et lichens). Les données européennes sont donc utilisables, d'autant plus que la simplicité de ces organismes les rend peu enclins à la différentiation génétique. Pour les conditions édaphiques, particulièrement le pH, les données de la littérature sont encore plus restreintes. Classiquement, pour le pH, on décrit les espèces comme étant calcicoles, neutrophiles et acidiphiles. Les données d'experts étant très difficiles à obtenir pour le pH, nous avons appliqué des régressions logistiques suivant le modèle de Laplace-Gauss sur des relevés issus d'études phytosociologiques faites à l'université Laval sous la direction du Professeur Miroslav Grantner. L'équation résultante de cette régression nous a permis de calculer la largeur de la distribution des espèces le long de ce gradient de pH. Cette dernière valeur, le kurtosis, permet d'avoir une idée de la plasticité des espèces vis-à-vis de ce gradient. Le même type d'analyse a été appliqué au gradient de lumière à l'aide du calcul de l'indice lumineux moyen obtenu suivant la valeur de tolérance à l'ombre des espèces présentes dans les relevés phytosociologiques. Quelque 96 espèces furent analysées de cette manière, et la régression nous a permis de dégager un indice de pH significatif pour 56 espèces et 51 espèces pour la lumière. L'analyse des résultats pour la plasticité nous a permis de dégager les patrons généraux de cette plasticité. La plasticité pour le pH varie selon une hyperbole négative en fonction de l'optimum écologique des espèces pour le pH. En d'autres termes, les espèces de milieu plus acide sont moins plastiques pour le pH, c'est-à-dire qu'elles se retrouvent sur des sols ayant une gamme de pH plus restreinte que les espèces de sol plus neutre. Ce résultat va dans le sens de l'hypothèse de spécialisation énoncée par Lortie and Aarssen (1996), à savoir que les espèces tendent à se spécialiser et cela au dépend de leur plasticité. Ce patron général ne se retrouve pas pour la lumière. Au contraire, il y a une très forte orthogonalité de la plasticité par rapport à son optimum. Cette orthogonalité indique que ces deux

caractéristiques pour la lumière ne sont pas en interaction et il se peut qu'il n'y ait pas de spécialisation pour la lumière. Les espèces dites tolérantes à l'ombre ne deviendraient donc pas plus tolérantes à l'ombre avec le temps, mais seraient plutôt confinées à de faibles conditions de lumière à cause de leur faible compétitivité dans les milieux adjacents plus lumineux. En conclusion, ce mémoire a permis de mieux caractériser les conditions écologiques générales d'un très grand nombre d'espèces par rapport à leur réaction au pH et à la lumière, deux conditions écologiques très importantes pour les plantes. De plus, la tolérance à l'ombre, qui indique classiquement le niveau de lumière où une plante subsiste, pourrait aussi être définie comme l'habileté compétitrice de cette espèce.

INTRODUCTION

Le maintient et la conservation de la diversité biologique passent par la connaissance des caractéristiques des êtres vivants et des interactions qui existent entre ces derniers. Le lien entre ces interactions et les caractéristiques des espèces est inévitablement très fort. Pour ce qui est des plantes, la phytosociologie (Braun-Blanquet, 1974) a permis de quantifier un tel lien. Elle suppose qu'à chaque habitat particulier correspond une association végétale particulière. Cette association varie évidemment à l'intérieur de cet habitat à cause de facteurs environnementaux comme la lumière, le pH, l'humidité du sol, etc. Mais la très grande variation dans le temps et l'espace des communautés végétales a rendu les études phytosociologiques peu efficaces. Afin d'aller plus loin, Ellenberg *et al.* (1992) ont caractérisé finement l'optimum écologique de plus de 5000 espèces européennes pour la lumière, le pH et la température, avec une échelle de valeur d'indices allant de 1 à 9 pour chacune des variables environnementales. Cet outil qui se base uniquement sur des données d'expert a vu son utilisation augmentée récemment dans le cadre des recherches faites sur le maintien de l'intégrité écologique des écosystèmes forestiers. Un tel outil a de nombreux avantages : un faible coût, il est facilement mis-en-oeuvre, il permet le suivi à long terme, etc. De plus, les applications d'un tel outil sont nombreuses, tant en foresterie (Schuck *et al.*, 1994) que pour la classification des sols (Wilson *et al.*, 2001), le suivi et la détection de la pollution (Ling, 2003) ou bien l'archéologie (Dupouey *et al.*, 2002). Un outil équivalent n'existant pas au Québec et en Amérique du Nord, le présent mémoire vise à évaluer la possibilité de développer un outil basé sur la caractérisation fine de l'optimum écologique des plantes de sous-bois du Québec et d'évaluer le lien entre l'amplitude écologique des plantes pour les deux variables écologiques qui vont être abordées (le pH et la lumière) avec cet optimum.

Nous avons choisi de nous concentrer sur la lumière et le pH car la répartition des plantes sur le globe, et plus localement, est fortement régie par ces facteurs environnementaux à l'intérieur d'une région donnée. Alors que la température et les précipitations régissent les patrons globaux de la répartition des espèces, la lumière et le pH permettent de distinguer les formations végétales régionales. La lumière est un facteur important de la répartition de la végétation forestière puisque la forêt possède une structure verticale très développée, ce qui affecte fortement l'environnement lumineux en sous-bois (Hutchinson and Matt, 1977). Les plantes vont exploiter ces variations de lumière de façon à optimiser la fixation du carbone. Par exemple, les printanières produisent leurs feuilles très tôt au printemps pour profiter de la lumière avant que le couvert se referme. La

sensibilité et l'efficacité des systèmes photosynthétiques vont distinguer les plantes entre elles et ainsi régir leur répartition sous des conditions de lumière différentes (Anderson *et al.*, 1969). La canopée est donc un facteur limitant pour la répartition des plantes forestières herbacées (Bratton, 1976), la tolérance à l'ombre indiquant alors jusqu'à quel niveau de faible lumière une plante peut survivre (Shirley, 1943). En outre, la lumière est un facteur qui a déjà été très largement étudié et nous pouvons utiliser ces études pour valider notre approche. Ainsi, Baker (1949) a caractérisé la tolérance à l'ombre des arbres en cinq classes, classification qui a eu un très gros impact sur le développement de la foresterie. Pour le pH, on utilise déjà les plantes comme indicateur de la fertilité des sols (Chapin, 1980; Peterson and Rolfe, 1981; Gilliam, 1988) et de nombreuses études (Siccama *et al.*, 1970; Gilliam and Turrill, 1993) traitent des variations de végétation selon un gradient de pH. Le pH est possiblement la variable qui caractérise le mieux le fonctionnement du sol, d'ailleurs on appelle le pH et ses variations, la réaction du sol. En général, le pH reflète la nature des colloïdes, la présence des ions Al^{3+} et Fe^{3+}, la nature des cations métalliques absorbés et la tension du CO_2 en sols calcaires (Duchaufour, 1982; Soltner, 2000). Enfin, le sol a un pouvoir tampon lié à la présence des colloïdes qui lui permet de résister à des variations de pH. Il est donc une composante intégrée et stable des sols.

Les études sur le terrain étant très coûteuses en temps et argent, nous avons pallié à ce problème par la mise sur pied d'un questionnaire auprès de forestiers et de botanistes chevronnés pour nous aider à caractériser la tolérance à l'ombre d'un très grand nombre d'espèces de sous-bois peu connues. Pour le pH, nous avons utilisé les données récoltées lors de relevés phytosociologiques et effectué des régressions logistiques gaussiennes pour déterminer la répartition des préférences de différentes espèces en terme de pH. De plus, des données issues de la littérature ont été compilées et confrontées à nos résultats pour fournir des indices les plus fiables possible.

CHAPITRE I

A SHADE TOLERANCE INDEX FOR COMMON UNDERSTORY SPECIES OF NORTHEASTERN NORTH AMERICA

Since Baker's (1949) classic contribution, shade tolerance indices have not been much modified for North American plant species. While many common tree and shrub species are included in the shade tolerance index, much less is known about this characteristic for the abundant and rich understory vascular and nonvascular plant layers. The classification of shade tolerance is widely used to compare relative growth and survival among plant species under closed canopies and is also fundamental to an understanding of stand development following small and large scale disturbances. Although qualitative, it is frequently used both in research and management implications. Here we provide a significant revision to Baker's shade tolerance table to include the most common forest understory plant species found in northeastern North American forests. Our index is based on (1) the compilation of the opinions of five experts, (2) a comparison with Ellenberg's index from Europe as well as (3) information from current literature. For most of the 347 plant species investigated, a consistent and robust shade tolerance index, ranging between 1 (very tolerant) and 9 (very intolerant), was found. Here we present revised shade indices for 71 tree and shrub species, 185 herbaceous species, and 91 bryophyte and lichen species.

1.1 Introduction

Light is one of the most studied ecological factors in plant ecophysiology due to its essential function autotrophic plants. It has been characterized under a wide variety of atmospheric conditions and under various plant covers (e.g. Hutchinson and Matt, 1977; Gendron *et al.*, 1998). We now know that not only its quantity, but also its quality and variability are important characteristics for plant growth. Similarly, many basic characteristics of plant functional acclimatation and adaptation to light have been reported (Messier *et al.*, 1999). However, even with our extensive documentation of the range of light conditions, the fundamental mechanisms of shade tolerance are still not fully understood (Lin *et al.*, 2001). What we know is that shade tolerance includes a suite of traits that can take different forms depending on the species and the environments. However, generally, shade tolerance indicates the degree to which a plant can survive and grow in low light conditions (Shirley, 1943; Kobe *et al.*, 1995), and plants have been classified into three broad categories : shade tolerant, intermediately shade tolerant and shade intolerant species (Anderson *et al.*, 1969). Although imperfect and rather coarse, such a classification has proven very useful in classifying trees into broad functional types (Baker, 1949).

However, useful such a classification has been for tree and shrub species, there is no North American equivalent for understory herbaceous plants, bryophytes and lichens. In Europe, Ellenberg (c.f. Ellenberg, 1979; Ellenberg *et al.*, 1992) has successfully characterized the shade tolerance of most plants using an index from 1 to 9. This classification has proven to be very useful not only to better understand the autecology of plant species, but also to use the presence or absence of various understory plant species as an indicator of understory light levels.

This paper proposes a shade tolerance index of common understory species present in the temperate hardwood forest of southern Quebec, Canada, and, in fact, common in northeastern North America.

1.2 Methods

An index of shade tolerance was developed for common forest understory species where shade tolerance was based on three independent sources of information. First, a group of five experts was surveyed and asked to rank the shade tolerance of a number of plant species (see below). Secondly, these responses were validated with published

information available for understory species, mostly studied in North America. Thirdly, these results were compared with the ranking proposed by Ellenberg in Europe for co-occurring species.

1.2.1 Using the opinions of experts

As with Baker (1949) and, more recently, Hess and King (2002), a questionnaire was sent to five expert plant ecologists who have extensive field experience with most plants found in the northeastern North American forest. The list included close to 400 species, including bryophytes and lichens. For woody species, only the seedling stage was considered.

The questionnaire required respondents to rank the light environment where the species grow and survive most commonly on a scale of one to five. The five levels were : (1) deep shade, (2) shade, (3) moderate shade, (4) partly open and (5) completely open. No indications of the light environment (percent of full sunlight) was required or requested. Due to the nature of the question, the answers did not provide a direct shade tolerance ranking, but rather an evaluation of the overall light environment in which the species were found to grow well. According to Brissot (1972), the light environment is the sum of three environmental factors : light, temperature and desiccation. In addition, the common occurrence of a species at a particular light level does not mean that this species is at its physiological optimum, but only that it is the best competitor in this environment. Consequently, we have determined the "ecological existence" not the "ecological potential" (Ellenberg, 1996; Whittaker *et al.*, 1973) of each plant species at a given light level.

All results were then adjusted to a nine level scale for comparisons with Ellenberg's index. This transformation did not change the mean of the values ; consequently, comparisons between data were not affected. An overall result was compiled from the questionnaires and the mean ($\overline{X}_e$) and standard deviation (σ_e) were calculated.

1.2.2 Using published data

Published results have focused primarily on the response of tree species, rarely are herbaceous species and bryophytes reported in shade-tolerance studies. In this paper, the following references were used : Grandtner (1997) ; Burns and Honkala (1990a,b) ; Minnesota Department of Transportation (2002) ; Ritchie (1996) ; Bakuzis and Hansen

(1959) ; Haussler and Coates (1986) ; Beaudry *et al.* (1999) ; Jobidon (1995) ; Ellenberg *et al.* (1992). The publication by Ellenberg *et al.* (1992) is important because of the vast number of species described and the strong correspondence between bryophytes in Europe and North America, as well as of some introduced vascular plants. The Ellenberg L index is based on phyto-sociological relevés combined with light measurements taken during the summer. Nearly 140 species, of which half are bryophytes, are present in both Quebec and Europe and could then be compared.
As with the previous section for the experts, all results were then adjusted to a nine level scale, the mean ($\overline{X}_p$) and the standard deviation (σ_p) were calculated.

1.2.3 Compilation

We chose to compile these data into a synthetical index based on the comparison of the mean and the standard deviation of the different sources. The kind of system used here is a hierarchical one which allows us to automatize the ranking, and the different levels in the hierarchy are used to optimize the usefulness of the data. We first classified results into two categories : homogeneous and non homogeneous, and this is done for the expert part of the data and the published part. This homogeneity is simply related to σ. When both expert and published data were homogeneous we compared means, and if the difference was no more than two, we used the expert result as the index. If not, this result was rejected and a second level of integration was conducted. This second level mixed together expert and published data. To do this we calculated σ, and as in the upper level (explained above) we deduced the homogeneity from it. When it was homogeneous, we took the $\overline{X}$ as the index. Rejected results were analysed in a final level case by case. When the general result was close (one or two points higher or lower) to the Ellenberg index we systematically chose the Ellenberg index. This choice was driven by the fact that Ellenberg's index is more precise (nine levels) compared to our questionnaire (five levels).

1.3 Results and discussion

1.3.1 Questionnaire and data from the literature

Table 1.1 shows a compilation of the classification given by the five experts. At least one expert evaluated all woody species, both tree seedlings and shrubs. The family Sali-

TAB. 1.1: Comparison between the original list of species, collected data and the resulting number of species with an attributed shade tolerant index value.

	Total species	Trees and shrubs	Herbaceous plants	Bryophytes and lichens
Original list	405	72	201	132
Botanist A	96	42	48	6
Botanist B	239	67	141	31
Botanist C	223	47	151	25
Botanist D	291	71	187	33
Botanist E	172	53	119	0
Published	128	57	57	14
Ellenberg	139	3	50	86
Synthetic index	347	71	185	91

caceae and the genus Amelanchier received the fewest responses. We received responses for nearly all the herbaceous species included in the survey. Only five species (2%) could not be evaluated by any of the experts. An additional 23 species (11%) received evaluations from only one expert. Among herbaceous plants, the Poaceae and Renonculaceae families received the fewest responses. Among the bryophytes, however, the response level was much lower, with no responses being provided for 74 species and only one answer for 34 other species.

The responses of the experts (Table 1.2) are very similar for 48% of the species and can be qualified as homogeneous. This homogeneity is defined by a low σ, in this case less than 1.75, 1.50, 1.25 and 1.00 depending on the number of responses. For 16% of the species, the responses of the experts are different ($\sigma_e > 2.25$), for 6% of the species the responses are very different ($\sigma_e > 3.00$).

From the literature reviewed, data was obtained for 128 species (57 woody species, 57 herbaceous species, and 14 bryophytes and lichens) (Table 1.1). However, 76 of these species (59%) were found in only one publication. Similar to the questionnaire, information from literature (Table 1.2) was homogeneous for 28% of the species, different for 4%, and very different for one species. In light of this variation, results from the experts and the literature were compared to produce a synthetic index (Column I in Table 1.2).

TAB. 1.2: Shade tolerance index for common understory species in the temperate hardwood forest of southern Quebec. Strata (Column Str) refers to Woody species (W=tree seedlings and shrubs), Herbaceous plants (H) and Bryophytes (M). Int column describe species native to Europe (€) and North American species introduced to Europe ($). n is the number of responses, σ the standard deviation and $\overline{X}$ the mean. The Ell. column lists the Ellenberg index. The last column, I, lists our proposed synthetic index and X indicates species with broad amplitudes.

Species			Experts			Literature			Ell.	I
	Str	Int	n	σ_e	$\overline{X_e}$	n	σ_p	$\overline{X_p}$		
Achillea millefolium	H	€	4	0	9	3	1.15	7.7	8	8
Actaea pachypoda	H		3	1.53	2.7					3
Actaea rubra	H		4	1.26	2.8	2	0	3		3
Adiantum pedatum	H		4	1	2.5					2
Ageratina altissima	H		3	1	6					6
Agrimonia gryposepala	H		2	3.54	5.5					X
Agrimonia striata	H		2	4.24	6					X
Agrostis capillaris	H	€	2	0	9	2	1.41	8	7	9
Agrostis gigantea	H	€	1		9				7	7
Anaphalis margaritacea	H		4	1	8.5					9
Anemone canadensis	H		3	1	8	1		7		8
Anemone virginiana var. alba	H		1		8					8
Antennaria parlinii ssp. fallax	H		1		9					9
Apocynum androsaemifolium	H		5	0.89	8.6	1		7		9
Aquilegia canadensis	H		2	0.71	8.5					8
Arabis drummondii	H		2	0	9					9
Aralia nudicaulis	H		5	1.67	4.6	1		3		5
Asplenium viride	H		4	3.65	5				4	4
Aster puniceus	H		4	2.58	6					X
Athyrium filix-femina	H		5	1.67	3.4	4	0.96	1.8	3	3
Botrychium virginianum	H		4	0	3				6	3
Calamagrostis canadensis	H		4	0	9	1		6		9
Calypso bulbosa	H		3	1.15	1.7					2
Cardamine diphylla	H		3	0.58	2.7					3
Carex arctata	H		4	1.71	3.3					3
Carex brunnescens	H		1		4				9	9
Carex communis	H		2	0.71	3.5					4
Carex deweyana	H		2	0.71	3.5					4
Carex intumescens	H		4	1.89	4.3					3
Carex pensylvanica	H		1		8	1		3		X
Carex retrorsa	H		1		9					9
Carex trisperma	H		2	1.41	6					6
Centaurea nigra	H	€	1		9	1		7	8	8
Chimaphila umbellata	H		4	0.96	3.8				4	4
Chrysosplenium americanum	H		2	1.41	4					4
Cinna latifolia	H		3	3.06	5.7	1		3		X
Circaea alpina	H		4	0.5	2.8	1		1	4	4
Cirsium muticum	H		3	1.15	7.7					8
Claytonia caroliniana	H		4	1	8.5					9
Clinopodium vulgare	H		2	2.83	7	1		7	7	7
Clintonia borealis	H		5	0.89	3.6					4

Species	Str	Int	n	σ_e	$\overline{X_e}$	n	σ_p	$\overline{X_p}$	Ell.	I
Coeloglossum viride var. virescens	H		2	0	3					3
Comandra umbellata ssp. umbellata	H		3	3.21	6.7					X
Conioselinum chinense	H		3	2.65	4					X
Coptis trifolia	H		5	0.45	3.2					3
Corallorhiza maculata	H		4	1	1.5					1
Corallorhiza trifida	H		5	1.67	2.6				x	3
Cryptogramma stelleri	H		2	2.83	5					X
Cypripedium acaule	H		4	1.89	4.3					3
Cystopteris bulbifera	H		3	1.53	3.3	1		3		3
Cystopteris fragilis	H		3	1	4				5	5
Danthonia spicata	H		3	2.31	7.7					9
Deschampsia flexuosa	H		2	0	9	1		7	6	9
Dicentra cucullaria	H		3	3.46	7					X
Draba arabisans	H		2	1.41	8					8
Drosera rotundifolia	H		4	1	8.5				8	8
Dryopteris carthusiana	H		5	1.1	2.8				5	3
Dryopteris marginalis	H		4	2.22	3.8					X
Elymus trachycaulus ssp. trachycaulus	H		2	1.41	8	1		7		8
Empetrum nigrum	H		4	0	9	1		7	7	9
Epigaea repens	H		4	2.31	5					X
Epilobium angustifolium	H		5	0	9	5	0.89	7.6	8	8
Epilobium ciliatum ssp. glandulosum	H	$	3	1.15	8.3					8
Epilobium palustre	H		3	2	7				7	7
Equisetum arvense	H		4	2.75	5.8	1		7	6	6
Equisetum hyemale	H		4	2.22	6.3	1		3	5	5
Equisetum pratense	H		3	2.65	6				5	5
Equisetum scirpoides	H		3	0.58	2.7					3
Equisetum sylvaticum	H		5	0.89	3.6	1		3	3	3
Eriophorum virginicum	H		4	0	9					9
Eupatorium maculatum	H		4	1	8.5	1		7		9
Eurybia macrophylla	H		4	1.63	5					6
Fragaria virginiana	H		5	0.89	8.6	1		5		9
Galeopsis tetrahit	H	€	5	1.1	8.2	1		9	7	7
Galium asprellum	H		5	2.61	5.4					X
Galium trifolium	H		5	2.19	3.6	1		3		X
Gaultheria hispidula	H		5	2.24	4	1		3		3
Gaultheria procumbens	H		5	2.19	5.4					X
Geum rivale	H		3	1.15	5.7	1		7	6	6
Glyceria striata	H		3	2	7				7	7
Goodyera oblongifolia	H		3	0	1	1		3		1
Goodyera repens	H		4	1.15	2	1		5		2
Gymnocarpium disjunctum	H		4	1.26	2.8					3
Heracleum sphondylium ssp. montanum	H		4	1	8.5	1		7	7	7
Hieracium caespitosum	H	€	3	0	9				8	8
Hieracium scabrum	H		3	1.15	8.3					8
Huperzia lucidula	H		5	0.89	2.6					3
Hypericum perforatum	H	€	4	1	8.5	1		8	7	7
Impatiens capensis	H		4	2.22	3.8					X
Iris versicolor	H		5	1.67	7.6					8
Lactuca biennis	H		4	2	8					9
Lactuca canadensis	H		2	0	9					9

Species	Str	Int	n	σ_e	$\overline{X_e}$	n	σ_p	$\overline{X_p}$	Ell.	I
Leucanthemum vulgare	H	€	4	0	9					9
Linnaea borealis	H		5	2.28	3.8				5	5
Listera convallarioides	H		4	1.63	3					3
Listera cordata	H		4	1.63	3				3	3
Lycopodium annotinum	H		5	0.89	4.4				3	3
Lycopodium clavatum	H		4	2.22	5.8				8	8
Lycopodium complanatum	H		4	1	4.5					5
Lycopodium obscurum	H		5	0.45	3.2					3
Lycopodium tristachyum	H		4	1.26	5.3					5
Maianthemum canadense	H		5	1.79	3.8	2	0	3		4
Maianthemum trifolium	H		4	1.91	7.5					8
Matteuccia struthiopteris	H		4	2.06	4.8				5	5
Medeola virginiana	H		4	1.26	2.8					3
Melampyrum lineare	H		4	1.5	5.8	1		3		5
Mentha arvensis	H		2	0.71	8.5	1		7	6	8
Mentha canadensis	H		2	0.71	8.5					8
Milium effusum	H		3	3.46	5	1		3	4	4
Mitchella repens	H		4	1.26	2.8					3
Mitella nuda	H		5	0.89	2.4					2
Moneses uniflora	H		4	0.96	2.3				4	4
Monotropa hypopithys	H		4	0.96	1.8	1		3		2
Monotropa uniflora	H		5	0.45	1.2	1		3		1
Onoclea sensibilis	H		5	1.79	5.2	1		3		5
Orthilia secunda	H		3	1	2	2	0	3	4	2
Oryzopsis asperifolia	H		4	1.5	4.3					4
Oryzopsis pungens	H		2	3.54	5.5					X
Osmorhiza berteroi	H		3	1.53	2.7					3
Osmorhiza longistylis	H		3	1.53	2.7					3
Osmunda cinnamomea	H		5	2.97	5.4	1		3		X
Osmunda claytoniana	H		4	2.22	4.3					5
Oxalis acetosella	H		4	1.63	3	1		1	1	1
Panicum acuminatum var. acuminatum	H		2	0	9					9
Pedicularis canadensis	H		2	4.24	4					X
Petasites frigidus var. palmatus	H		4	3.46	6	1		2		X
Phegopteris connectilis	H		4	1.26	2.8					3
Platanthera dilatata var. dilatata	H		2	2.83	5					X
Platanthera obtusata	H		3	1.15	3.7					4
Platanthera orbiculata	H		3		3	1		3		3
Poa interior	H		1		9					9
Polygala paucifolia	H		4	3.3	4.8					X
Polygonatum pubescens	H		4	2.5	3.8					X
Polypodium virginianum	H		4	1.26	2.8	1		3		3
Polystichum braunii	H		4	1.63	3				3	3
Polystichum lonchitis	H		3	0	3				6	3
Potentilla norvegica	H		4	1	8.5				7	7
Potentilla recta	H	€	1		9				9	9
Potentilla simplex	H		1		9					9
Prenanthes altissima	H		4	3.4	4.3					X
Prenanthes trifoliolata	H		3	1.53	2.7					3
Prunella vulgaris	H		4	3.46	6	1		9	7	7
Pteridium aquilinum	H		3	1.15	7.7	3	1.73	6	6	6

Species	Str	Int	n	σ_e	$\overline{X_e}$	n	σ_p	$\overline{X_p}$	Ell.	I
Pteridium aquilinum var. latiusculum	H		4	1.63	7	2	2.83	5		7
Pyrola asarifolia	H		4	0.5	2.8					3
Pyrola chlorantha	H		3	1.15	3.7	1		5		4
Pyrola elliptica	H		5	0.89	3.6					4
Pyrola rotundifolia	H		5	1	4	1		3	4	4
Ranunculus abortivus	H		3	1.15	6.3					6
Ranunculus acris	H	€	3	0	9				7	9
Ranunculus repens	H	€	2	2.83	7	1		5	6	6
Rubus allengheniensis	H		2	0	9					9
Rubus chamaemorus	H		4	1.15	8				9	9
Rubus idaeus	H		5	0.89	8.4	5	1.1	7.2	7	7
Rubus pubescens	H		5	1.67	3.4					3
Rumex aquaticus var. fenestratus	H		2	0	9					9
Sanguisorba canadensis	H		4	1	8.5	1		3		9
Sanicula marilandica	H		3	2.52	3.3					4
Saxifraga paniculata ssp. neogaea	H		4	0	9					9
Schizachne purpurascens	H		3	2.31	7.7	1		5		9
Scutellaria lateriflora	H		4	2.06	5.3					X
Senecio aureus	H		1		9					9
Smilacina racemosa	H		4	1.89	4.3					3
Solidago hispida	H		3	2	7					6
Solidago juncea	H		1		9					9
Solidago macrophylla	H		4	3	5.5					X
Solidago rugosa	H		4	1.63	7					7
Streptopus amplexifolius	H		4	1.63	3				5	5
Streptopus lanceolatus var. roseus	H		3	1.15	3.7					4
Taraxacum officinale	H	€	5	0	9	1		9		9
Thalictrum pubescens	H		4	1.15	4					4
Thelypteris noveboracensis	H		4	2.5	3.8					X
Trientalis borealis	H		5	0.89	3.4	1		3		3
Trillium cernuum	H		5	1.41	3					3
Trillium erectum	H		4	1.91	4.5					4
Trillium undulatum	H		3	0	3					3
Urochloa xantholeuca	H		1		9					9
Viola adunca	H		1		7	1		6		7
Viola cucullata	H		1		3					3
Viola incognita	H		3	0	3					3
Viola macloskeyi ssp. pallens	H		4	1	3.5					3
Viola pubescens	H		3	1.15	3.7					4
Viola renifolia	H		4	1	3.5					3
Viola selkirkii	H		3	1.15	3.7					4
Waldsteinia fragarioides	H		3	1.53	6.7					7
Aulacomnium palustre	M		1		3	1		7	7	7
Barbilophozia barbata	M								8	8
Barbilophozia hatcheri	M								6	6
Bazzania trilobata	M		3	1.15	2.3				5	3
Blepharostoma trichophyllum	M								5	5
Brachythecium populeum	M								4	4
Brachythecium reflexum	M								4	4
Brachythecium rutabulum	M									X
Brachythecium salebrosum	M		1		3				6	6

Species	Str	Int	n	σ_e	$\overline{X_e}$	n	σ_p	$\overline{X_p}$	Ell.	I
Brachythecium velutinum	M								5	5
Buellia disciformis	M		1		9				4	4
Callicladium haldanianum	M								6	6
Calypogeia neesiana	M								5	5
Campylium chrysophyllum	M								9	9
Campylium stellatum	M								8	8
Cladina rangiferina	M		2	0	9	1		3		X
Cladina stellaris	M		3	1.15	8.3					8
Cladonia cenotea	M								6	6
Cladonia coniocraea	M		1		3				5	5
Cladonia deformis	M								7	7
Cladonia mitis	M		3	1.15	8.3				9	9
Cladonia rangiferina	M		3	1.15	8.3				6	8
Cladonia squamosa	M								6	6
Cladonia uncialis	M		1		9				8	8
Climacium dendroides	M		2	1.41	2				7	7
Dicranum flagellare	M		1		3				6	6
Dicranum fuscescens	M		3	1.15	2.3				7	2
Dicranum majus	M					1		1	5	5
Dicranum montanum	M		2	0	3				6	3
Dicranum polysetum	M		2	2.83	5				6	6
Dicranum scoparium	M		2	1.41	2				5	5
Eurhynchium pulchellum	M		2	0.71	4.5				6	6
Graphis scripta	M								3	3
Herzogiella striatella	M								6	6
Heterocladium dimorphum	M								8	8
Hylocomium splendens	M		4	1.26	2.8	2	1.41	4	6	3
Hypnum lindbergii	M								8	8
Hypnum pallescens	M								5	5
Hypnum pratense	M								8	8
Hypogymnia physodes	M		1		1				7	7
Hypogymnia tubulosa	M								7	7
Jungermania leiantha	M		1		7				4	4
Lepidozia reptans	M								4	4
Leucobryum glaucum	M		1		3				5	5
Lobaria pulmonaria	M		2	4.24	6				5	5
Marchantia polymorpha	M		3	3.61	4	1		7	8	8
Mnium spinulosum	M								5	5
Neckera pennata	M								5	5
Oncophorus wahlenbergii	M								5	5
Paraleucobryum longifolium	M		1		3				4	4
Parmelia saxatilis	M								6	6
Parmelia sulcata	M								7	7
Parmeliopsis ambigua	M								6	6
Peltigera aphtosa	M		2	2.83	5					X
Peltigera canina	M		2	2.83	5				6	6
Peltigera horizontalis	M								5	5
Peltigera leucophlebia	M		1		6				5	5
Pertusaria amara	M								6	6
Plagiochila asplenioides	M					1		3	4	4
Plagiothecium denticulatum	M								5	5

Species	Str	Int	n	σ_e	$\overline{X_e}$	n	σ_p	$\overline{X_p}$	Ell.	I
Plagiothecium laetum	M		1		3				4	4
Platismatia glauca	M		1		3				7	7
Pleurozium schreberi	M		3	2.52	5.3	1		7	6	6
Pohlia nutans	M								5	5
Polytrichum commune	M		4	1.5	6.3				7	7
Polytrichum formosum	M					1		3	4	4
Polytrichum juniperinum	M		2	1.41	8	1		7	8	8
Polytrichum piliferum	M		2	0	9				9	9
Ptilidium ciliare	M		1		3				8	8
Ptilidium pulcherrimum	M								7	7
Ptilium crista-castrensis	M		3	1.15	2.3	1		3	4	4
Radula complanata	M								7	7
Ramalina fastigiata	M								7	7
Rhizomnium magnifolium	M		1		3				5	5
Rhytidiadelphus triquetrus	M		3	4.16	4.3	1		3	7	7
Sphagnum centrale	M		1		5				6	6
Sphagnum fuscum	M		2	1.41	8				9	9
Sphagnum girgensohnii	M		1		3	1		3	4	4
Sphagnum magellanicum	M		1		5				9	9
Sphagnum rubellum	M		1		7				9	9
Sphagnum russowii	M		1		5				6	6
Sphagnum squarrosum	M		1		3	1		5	5	5
Tetraphis pellucida	M								3	3
Thuidium delicatulum	M		2	1.41	2				7	7
Thuidium recognitum	M								5	5
Tortella tortuosa	M								5	5
Trichocolea tomentella	M		1		1				6	6
Ulota coarctata	M								6	6
Ulota crispa	M								4	4
Usnea filipendula	M		1		9					9
Usnea subfloridana	M		1		9				7	7
Abies balsamea	W		4	0	3	4	1.26	2.8		3
Acer pensylvanicum	W		2	1.41	4	2	0	1		3
Acer rubrum	W		4	1	5.5	6	1.67	5		5
Acer saccharum	W		4	1.15	4	4	0.5	1.3		4
Acer spicatum	W		5	1.48	5.2	4	1.26	3.3		5
Alnus incana ssp. rugosa	W		5	1.48	7.2	6	1.75	6.3		7
Alnus viridis ssp. crispa	W		5	1.67	7.6	2	2.12	6.5		8
Amelanchier alnifolia	W		2	1.41	8	2	0.71	7.5		8
Amelanchier arborea	W		3	2.52	5.3	1		1		X
Amelanchier bartramiana	W		3	1.53	6.7					7
Amelanchier laevis	W		3	2.52	5.3	2	0	1		X
Amelanchier sanguinea var. gaspensis	W		3	2.08	7.3	1		8		8
Amelanchier sanguinea var. sanguinea	W		2	2.12	6.5	2	3.54	5.5		X
Andromeda polifolia var. glaucophylla	W		4	1	8.5	1		9		9
Aronia melanocarpa	W		4	1	8.5	1		7		9
Betula alleghaniensis	W		5	1.48	5.2	5	1.64	3.8		5
Betula papyrifera	W		2	0	7	8	1.13	7.1		7
Cassandra calyculata	W		5	1.79	7.8					8
Chamaedaphne calyculata	W		3	1.15	8.3	2	1.41	8	7	7
Comptonia peregrina	W		5	1.67	7.4					7

Species	Str	Int	n	σ_e	$\overline{X_e}$	n	σ_p	$\overline{X_p}$	Ell.	I
Cornus alternifolia	W		5	1.67	3.6	1		1		4
Cornus canadensis	W		5	1.67	4.6	2	2.83	3		X
Cornus sericea ssp. sericea	W	$	5	1.67	6.6	1		9		7
Corylus cornuta	W		4	0.96	3.8	3	1.73	6		4
Diervilla lonicera	W		5	1.79	5.8	1		7		6
Fagus grandifolia	W		3	2.31	4.3	3	0.58	1.3		2
Fraxinus nigra	W		4	0	5	5	2.59	5.8		5
Ilex mucronata	W		5	1.79	5.8					5
Kalmia angustifolia	W		5	2	7	1		3	8	8
Kalmia polifolia	W		5	1.79	7.8					8
Larix laricina	W		4	0	9	6	0.52	8.7		9
Ledum groenlandicum	W		5	1.41	7	4	1.5	7.8		7
Lonicera canadensis	W		5	2	3					X
Myrica gale	W		5	0	9				8	8
Ostrya virginiana	W		2	2.83	5	5	1.34	2.4		X
Picea glauca	W		4	1.15	4	4	1.29	4.5		4
Picea mariana	W		4	2.31	5	5	1.82	4.6		X
Pinus banksiana	W		5	0.45	8.8	5	1.67	7.6		9
Pinus resinosa	W		4	1	8.5	5	1.22	7		8
Pinus strobus	W	$	4	1.15	6	6	1.03	5.3		6
Populus balsamifera	W		4	0	9	6	1.1	8		9
Populus grandidentata	W		4	0	9	5	1.22	8		9
Populus tremuloides	W		3	0	9	8	0.83	8.1		9
Prunus pensylvanica	W		4	1	8.5	4	0.5	8.8		9
Prunus serotina	W	$	2	1.41	8	5	2	6		8
Prunus virginiana	W		5	2.41	3.6	2	0.71	7.5		X
Quercus rubra	W	$	5	1.1	6.8	4	1.29	5.5		7
Ribes glandulosum	W		5	1.79	3.8	1		5		4
Ribes hirtellum	W		4	1.91	3.5					4
Ribes lacustre	W		5	1.41	3	1		6		3
Ribes triste	W		4	2.52	3.5					3
Rosa acicularis	W		4	2.87	7.3					X
Salix bebbiana	W		4	1.15	8	4	0.82	8		8
Salix discolor	W		2	1.41	8	2	0.71	8.5		8
Salix eriocephala	W		1		9					9
Salix humilis	W		1		9	1		9		9
Sambucus racemosa ssp. pubens	W		4	1.71	4.8	2	1.41	6		5
Shepherdia canadensis	W		3	1.15	8.3	1		9		8
Sorbus americana	W		5	0.89	5.4	1		8		5
Sorbus decora	W		4	1.91	6.5	2	2.83	7		X
Taxus canadensis	W		5	0.89	1.6	1		3		2
Thuja occidentalis	W		5	1.67	3.4	4	2.16	4		3
Tsuga canadensis	W		3	2	3	4	0.96	1.8		3
Ulmus americana	W		3	2	7	4	1.71	5.3		6
Vaccinium angustifolium	W		5	1.79	6.8	1		3		7
Vaccinium myrtilloides	W		5	2.68	6.8					X
Vaccinium ovalifolium	W		3	2	3	2	0	1		3
Vaccinium oxycoccos	W		4	2.83	7	1		9		X
Viburnum cassinoides	W		4	2.22	5.8					X
Viburnum edule	W		4	3.42	5.5	2	2.12	5.5		X

Species	Str	Int	n	σ_e	$\overline{X_e}$	n	σ_p	$\overline{X_p}$	Ell.	I
Viburnum opulus var. americanum	W		3	2	7					7

1.3.2 Comparisons

Comparisons between the published data and the expert opinions show a difference greater or equal to three light levels for 19 species. Eight of these are woody species : *Acer pensylvanicum, Amelanchier arborea, Amelanchier laevis, Fagus grandifolia, Kalmia angustifolia, Prunus virginiana, Ribes lacustre* and *Vaccinium angustifolium.* There was, however, little data for the genus Amelanchier which may explain its high variability. *Acer pensylvanicum* and *Prunus virginiana* are non-commercial species and were not well documented in published data. The case of *Fagus grandifolia* is different because only one divergent response was given compared to five homogeneous ones. Thus, without this one "outlier" point, the result is very good. Furthermore, the value for *Fagus grandifolia* did match Ellenberg's index for *Fagus sylvatica.* The herbaceous species that were treated in the literature included *Calamagrostis canadensis, Carex pensylvanica, Equisetum hyemale, Fragaria virginiana, Goodyera repens, Petasites frigidus* var. *palmatus, Prunella vulgaris* and *Sanguisorba canadensis.* There was a high variation in classification and this is probably due to lack of data and the fact that some families are not well-known (e.g. Poaceae). The same was true for the bryophytes and lichens (*Aulacomnium palustre, Cladina rangiferina* and *Marchantia polymorpha*).

Ellenberg *et al.* (1992) provides comparable data for three woody species, 50 herbaceous species and 86 bryophytes and lichens. The bryophyte layer alone contains 42 species for which we found no North American data, and four other species that have no American counterpart. In most cases the value obtained for North America is lower than Ellenberg's index, but given that there are few data we feel that it is not appropriate to reject Ellenberg's value and thus we preferred to use the Ellenberg value as a final index. However, this should be taken into account when applying the index, and further testing of the given value and the North American result should be pursued. For woody and herbaceous species, there is a strong similarity between Ellenberg's index and the experts' responses reported here. It is similar for 64% of the species (difference < 1.50), and very similar for 26% (difference < 1.00), with only 9% of species that were very different. Some of the vascular species are native to Europe but were introduced to North America (Rousseau, 1968, 1974) : *Achillea millefolium, Agrostis*

capillaris, Agrostis gigantea, Centaurea nigra, Galeopsis tetrahit, Hieracium caespitosum, Hypericum perforatum, Leucanthemum vulgare, Potentilla recta, Ranunculus acris, Ranunculus repens and *Taraxacum officinale*. Only the results for *Agrostis capillaris* and *Ranunculus acris* show a two point difference with Ellenberg, whereas the others species are similar to the European index. There are also North American species that were introduced in Europe : *Cornus sericea* ssp. *sericea*, *Epilobium ciliatum* ssp. *glandulosum, Pinus strobus, Prunus serotina* and *Quercus rubra*. Ellenberg has investigated *Epilobium ciliatum* ssp. *glandulosum* and *Prunus serotina*, and his results are similar to those obtained here, with a difference of one point and two points respectively. Surprisingly, Landolt (1977) gives a light level value of three in a nine level scale for *Prunus serotina*, that can be substantial since this species invades forest understories and supresses regeneration of other species (Starfinger, 1991; Starfinger, 1997; Starfinger *et al.*, 2003). However, this behaviour may be simply a transitional stage. He also investigates *Quercus rubra*, and his ranking was identical to ours and that of Gerhard Karrer (personal communication). However, *Cornus sericea* ssp. *sericea* seems to be very shade tolerant in Europe (Landolt, 1977). No European data were found for *Pinus strobus*.

Some species have a world-wide distributions and are consequently found in the Northern hemisphere as well as in the Southern hemisphere, such as *Cystopteris fragilis*, *Deschampsia flexuosa*, *Dryopteris carthusiana* and *Equisetum arvense* (Rousseau, 1974). For these species, expert responses and published data are similar to the European data. In the case of *Deschampsia flexuosa*, we used no published data, Rameau *et al.* (1989) who indicated a rank of mid-tolerant to intolerant, which is consistent with our ranking. Interestingly, all of these species are mid-tolerant and are found generally at the edge of forest paths. In the case of *Deschampsia flexuosa* Rameau *et al.* (1989) indicated a rank of mid-tolerant to intolerant and a wide range of different habitats such as forests of oak, beech, pine, alpine meadows or moors, which is consistent with our ranking. However, in Central Europe this species seems to be more shade tolerant and the corresponding Ellenberg's value is 6. As well as *Deschampsia flexuosa*, *Dryopteris carthusiana* has a wide range of habitats from pine forests and deciduous forests, to moors in Europe (Rameau *et al.*, 1989). And as in Europe these species also covered a wide range of habitats in North America.

Other co-occuring species are either world-wide in distribution or they are circumboreal species, as is the case for most of the bryophytes and some of the vascular species (e. g. *Linnaea borealis*). It is possible that some are invasive species, but during the last 30 years the new intruders in North America originate mostly from Asia and have mostly become established along coasts and rivers, and not in forested areas (Claudi *et*

al., 2002).

1.3.3 Examples of ranking

In many cases the general rule failed to give a consistent index, but we tried to capitalize on all of the available data. This task was done by studying each species case by case. As stated before for *Fagus grandifolia*, we obtained an answer outside of the range which drove the standard deviation away from our selection criteria. Raw results for experts were 3, 3 and 7, and for published data they were 1, 1 and 2. $\overline{X}$ are respectively 4.3 and 1.3 with σ equal to 2.3 and 0.6, and since these values do not match, the overall σ (2.23) is still too high. In this case we chose to eliminate the outlier, and an index of 2 was assigned. Concerning the choice between our results and Ellenberg's, two different cases appear. The first one is when our result is within two points of Ellenberg's, the second occurs when the difference is greater than two. The first case can be illustrated by the results for *Equisetum hyemale*. The raw data were 7, 5, 4 and 9 for the expert opinion, which gives a mean response of 6.3. This can be contrasted with one published datum with a value of 3 and with Ellenberg's, value of 5. In this case, our result is near Ellenberg's but as mentioned earlier, Ellenberg used a nine point scale level whereas we used a five point scale, which must then be expanded to nine for our results. Consequently, in cases of contrasts we favoured the more precise Ellenberg index. However, in the second case, our results are prefered and thus indicate a difference between the continents.

1.3.4 Robustness and adaptability

The procedure presented here has been applied to reduce or level out subjective interpersonal differences, but also to address smaller interspecific differences due to genetics or other geographical differences in ecological behaviour. The diversity of information that is integrated, experts' opinions as well as published data, make this index robust and widely applicable. This is the main difference with the Ellenberg approach (which is based primarily on experts' opinions and which has led to much criticism (Dierschke, 1994). The approach by indicator values has been extensively discussed (see Diekmann (2003) for a review), but despite criticism it is stated that "the beauty of the system lies in its generality and robustness" (Ewald, 2003). Moreover, it is possible to calibrate the values obtained for other parts of North America. Such a calibration has been made on

Ellenberg's Central Europe indices for Britain (Hill *et al.*, 1999, 2000), Sweden (Diekmann, 1995; Diekmann and Falkengren-Grerup, 1998), the Netherlands (Schaffers and Sykora, 2000) and Denmark (Lawesson and Mark, 2000). The methods they used have improved Ellenberg's values, and this is supported by the good correlation among all of these studies (Diekmann, 2003).

1.4 Conclusion

Our goal was to develop a shade tolerance index for understory plant species in northeastern North America as was done by Ellenberg *et al.* (1992) in Europe. An index was developed that will be consistent, robust and widely applicable. However, we acknowledge that the ecological preference of a species can vary within its geographical range. As stated before, the "ecological existence" was evaluated and not the "ecological potential" (Ellenberg, 1996; Whittaker *et al.*, 1973) of each species, the former reflecting the ability of a species to generally persist at a given light level. If the light conditions change, the species may survive under stress for quite a long time. Consequently, this index should be used with caution when attempting to characterize light conditions using understory species as indicators.

BIBLIOGRAPHIE

Anderson R. C., Loucks O. L., Swain A. M., 1969. Herbaceous response to canopy cover, light intensity and through fall precipitation in coniferous forests. Ecology 50(2) : 255-263.

Baker F. S., 1949. A revised tolerance table. J. For. 47 : 179-181.

Bakuzis E.V., Hansen H.L., 1959. A provisional assessment of species synecological requirement in Minnesota forests. Univ. Minn., St. Paul, Minn., Minn. For. Notes No. 84. 2 p.

Beaudry L., Coupé R., Delong C., Pojar J., 1999. Plant Indicator Guide for Northern British Columbia : Boreal, Sub-Boreal and Subalpine Biogeoclimatic Zones (BWBS, SBS, SBPS and northern ESSF). British Columbia Ministry Forests Research. 139 p.

Brissot M., 1972. Rachitisme ou coup de soleil ? Forêt Privée Francaise 87 : 27-34. (in French)

Burns R.M., Honkala B.H., 1990a. Silvics of North America : 1. Conifers. Agriculture Handbook 654. U.S. Department of Agriculture, Forest Service, Washington, DC. vol.1, 650 p.

Burns R.M., Honkala B.H., 1990b. Silvics of North America : 2. Hardwoods. Agriculture Handbook 654. U.S. Department of Agriculture, Forest Service, Washington, DC. vol.2, 877 p.

Claudi R., Nantel P., Muckle-Jeffs E., 2002. Alien Invaders in Canada's Waters, Wetlands, and Forests. Natural Resources Canada, 320 p.

Diekmann M., 1995. Use and improvement of Ellenberg's indicator values in deciduous forests of the Boreo-nemoral zone in Sweden. Ecography 18 : 178–189.

Diekmann M., Falkengren-Grerup U., 1998. A new species index for forest vascular plants : development of functional indices based on mineralization rates of various forms of soil nitrogen. Journal of Ecology 86 : 269–283.

Diekmann M., 2003. Species indicator values as an important tool in applied plant ecology : a review. Basic Appl. Ecol. 4 : 493–506.

Dierschke H., 1994. Pflanzensoziologie. Eugen Ulmer Verlag, Stuttgart. 683 p. (in German)

Ellenberg H., 1979. Indicator values of vascular plants in Central Europe. Scripta Geobotanica 9 : 7-122.

Ellenberg H., 1996. Vegetation Mitteleuropas mit den Alpen. 5 Aufl. Eugen Ulmer Verlag, Stuttgart. 1095 p. (in German)

Ellenberg H., Weber H.E., Düll R., Wirth V., Werner W., Paulissen D., 1992. Zeigerwerte von Pflanzen in Mitteleuropa. Scripta Geobotanica 18 : 1-258. (in German)

Ewald J., 2003. The sensitivity of Ellenberg indicator values to the completeness of vegetation relevés. Basic Appl. Ecol. 4 : 507–513.

Gendron F., Messier C., Comeau P.G., 1998. Comparison of various methods for estimating the mean growing season percent photosynthetic photon flux density in forests. Agric. For. Meteorol. 92 : 55-70.

Grandtner M., 1997. World Dictionary of Trees (available on-line the 15 February 2005 at http ://www.wdt.qc.ca/)

Haussler S., Coates D., 1986. Autecological Characteristics of Selected Species that Competewith Conifers in British Columbia : Literature review. FRDA Report, ISSN 0835-0752 ; 001.

Hess G.R., King T.J., 2002. Planning open spaces for wildlife. I. Selecting focal species using a Delphi survey approach. Landscape Urban Plann. 58 : 25-40.

Hill M.O., Mountford J.O., Roy D.B., Bunce R.G.H., 1999. Ellenberg's indicator values for British plants. Institute of Terrestrial Ecology, Huntingdon, UK.

Hill M.O., Roy D.B., Mountford J.O., Bunce R.G.H., 2000. Extending Ellenberg's indicator values to a new area : an algorithmic approach. Journal of Applied Ecology 37 : 3–15.

Hutchinson B.A., Matt D.R., 1977. The annual cycle of solar radiation in a deciduous forest. Agric. Meteorol. 18 : 255–265

Jobidon R., 1995. Autécologie de quelques espèces de compétition d'importance pour la régénération forestière au Québec. Revue de la littérature. RNCanada Report No. 117, 179 p. (in French)

Kobe R.K., Pacala S.W., Silander J.A., Canham C.D., 1995. Juvenile tree survivorship as a component of shade tolerance. Ecological Applications 5 : 517–532.

Landolt E., 1977. Oekologische Zeigerwerte zur Schweizer Flora. Veröff. Geobot. Inst. ETH Rübel, Zürich, 64, 206 pp. (in German)

Lawesson J.E., Mark S., 2000. pH and Ellenberg reaction values for Danish forest plants. In : White P.S., Mucina L., Leps J. (eds) Vegetation science in retrospect and perspective. Proceedings IAVS Symposium, Uppsala, pp. 153–155.

Lin J., Harcombe P. A., Fulton M. R., 2001. Characterizing shade tolerance by the relationship between mortality and growth in tree saplings in a southeastern Texas forest. Can. J. For. Res. 31 : 345–349.

Messier C., Doucet R., Ruel J-C., Kelly C., Lechowicz M.J., 1999. Functional ecology of advance regeneration in relation to light in boreal forests. Can. J. For. Res. 29 : 812–823.

Minnesota Department of Transportation, 2002. Plant Selector (available on-line the 15 February 2005 at http ://plantselector.dot.state.mn.us/)

Rameau J.-C., Mansion D., Dumé G., 1989. Flore forestière française Vol.1 : plaines et collines. Institut Pour Le Developpement Forestier, Paris. 1794 p. (in French)

Ritchie G.A., 1996. Trees of Knowledge : a handbook of Maritime Trees. Canadian forest service Fo42-244/1996 English edition.

Rousseau C., 1968. Histoire, habitat et distribution de 220 plantes introduites au Québec. Naturaliste Can. 95 : 49–169. (in French)

Rousseau C., 1974. Géographie floristique du Québec-Labrador. Distribution des principales espèces vasculaires. Travaux et Documents du centre d'études nordiques 7, University Laval Press, 800 p. (in French)

Schaffers A.P., Sykora K.V., 2000. Reliability of Ellenberg indicator values for moisture, nitrogen and soil reaction : a comparison with field measurements. Journal of Vegetation Science 11 : 225–244.

Shirley H.L., 1943. Is tolerance the capacity to endure shade? J. For. 41 : 339–345.

Starfinger U., 1991. Population biology of an invading tree species - Prunus serotina. In : Seitz, A. and Loeschke, V. (eds.) Species conservation : a population-biological approach. Birkhäuser, Basel, Switzerland, pp. 171–184.

Starfinger U., 1997. Introduction and naturalization of Prunus serotina in Central Europe. In : Brock, J.H., Wade, M., Pysek, P., and Green, D. (eds.) Plant invasions : Studies from North America and Europe. Backhuys Publishers, Leiden, pp. 161–171.

Starfinger U., Kowarik I., Rode M., Schepker H., 2003. From Desirable Ornamental Plant to Pest to Accepted Addition to the Flora?? the Perception of an Alien Tree Species Through the Centuries. Biological Invasions 5(4) : 323–335.

Whittaker, R. H., Levin S. A., Root R. B., 1973. Niche, habitat, and ecotype. Am. Nat. 107 : 321–338.

CHAPITRE II

SPECIALIZATION ALONG ENVIRONMENTAL GRADIENTS IN THE FOREST UNDERSTORY

General patterns of species plasticity or niche breadth along ecological gradients are not well understood. Although several hypotheses have been proposed, few studies and with only a limited number of species have verified these theories in the field. Here, we investigate the relationship between environmental preference and niche breadth of forest understory plant species for light and pH. We assume that species distribution follows the realized niche concept. The preference of the realized niche and the kurtosis of this distribution were derived from Gaussian logistic regression. The kurtosis of the curve is used in this study as a measure of niche breadth. The niche breadth relation was mainly related to pH and not to light. The relationship of niche breadth and pH followed a negative hyperbolic curve. Our results support the specialization hypothesis for pH but not for light, and indicate that adaptations to extreme pH are more constraining on species distribution than to extreme light. Our results also suggest that forest understory plants do not specialize for shade or full sunlight, but rather some species tolerate low light and are maintained or displaced by competition. We suggest then that in forest understories, such as those of the northeastern temperate forests, plant species distribution is mainly constrained by pH rather than light.

2.1 Introduction

Species plasticity, or niche breadth, is defined as the ability of that species to adapt to variations in environmental conditions. Such plasticity can then be viewed as the ability of a species to adapt, and therefore grow and survive, in a wide range of habitats. This is often described as the fundamental niche concept (Hutchinson, 1957) where the niche of a certain species is defined by the extent of all environmental conditions that allows that species to compensate for its death rate by its birth rate (Chase and Leibold, 2003). Plasticity can also be considered as the number of ecotypes for a given species (Whittaker *et al.*, 1973). Plasticity is often referred to in terms of the phenotypic variation that occurs within certain temporal and local variations in the environment (Bradshaw, 1965; Schlichting and Pigliucci, 1998; Agrawal, 2001; Givnish, 2002). In this case, plasticity implies that phenotypic variations will not be transmitted, or only for some rare cases, to the next generation (Agrawal *et al.*, 1999; Van Dam and Baldwin, 2001; Karban *et al.*, 2000). In this study, we are interested in the concept of niche plasticity. We agree with Givnish (2002) who states that a proper search for a general relationship between plasticity and niche breadth has yet to be conducted. We use the term niche breadth to refer to the proportion of environmental gradient over which a species can be found.

Our main objective is to determine whether or not the niche breadth of forest understory plant species depends on species preferences along environmental gradients and, if it does, how it differs between two important ecological gradients : light and pH. We also test the hypothesis formulated by Lortie and Aarssen (1996) that genotypes subjected to a strong habitat selection are more likely to develop ecotypic differentiation. Lortie and Aarssen (1996) call this the specialization hypothesis, where specialists are better competitors than generalists in certain special environments, but they are less plastic and consequently less able to colonize many different environments or survive in environments with heterogeneous conditions (Valladares *et al.*, 2000; Alpert and Simms, 2002). This hypothesis also suggests that species having a wider niche breadth would be at an advantage in habitats where environmental conditions are higher overall (Alpert and Simms, 2002). These hypotheses can be summarized using a curve (Figure 2.1) that follows a hypothetical bi-directional gradient. In each direction, the niche breadth of a species decreases suddenly at the end of a gradient. We expect to find a greater niche plasticity for the most constraining environmental conditions, for example pH and light.

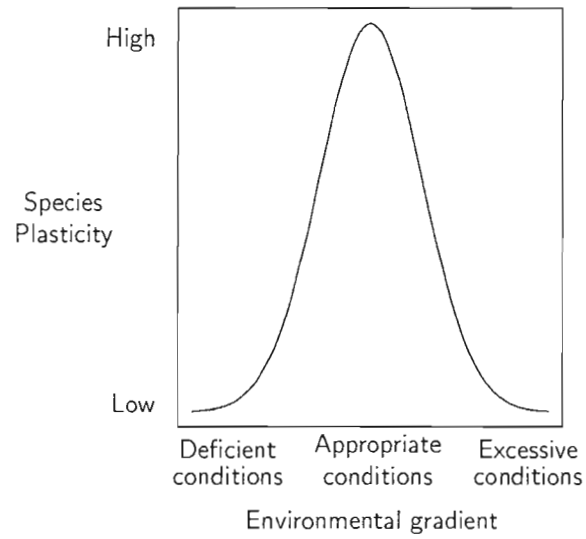

FIG. 2.1: Hypothesized variation in niche breadth along a bi-directional environmental gradient

2.2 Methods

2.2.1 Data

For this study, we used data on forest understory plant species published in the literature. One of the main problems with using published data is the heterogeneity in methods used by various authors. Consequently, to circumvent this, we used ecological studies conducted in one region (province of Quebec, Canada) by Grandtner (1969) and co-workers under his direction : Brown (1981); Majcen (1981); Bergeron *et al.* (1985). The methodology they used to sample the forest understory is greatly inspired by Braun-Blanquet's (1964) phytosociological method. The principle behind this approach is to describe ecotypes by associations of characteristic plants assuming that only one association will be related to a given ecotype. The main tool used in this method was very precise vegetation relevés. The selected studies evaluated understory plant cover in a wide range of forest cover types and pH was determined in the laboratory. Compilation of the data on plant abundance from these studies provided us with more than 400 relevés regrouping more than 1000 observations (one relevé can be an average of observations made in the same phytosociological type) and have been transformed to presence/absence data. Additionally, these studies provided information

from a large cross-section of forests types found in northeastern North America, which should make allow us to more readily generalize the results. Data on pH was directly available from these studies. Since light was not measured in these studies it was estimated using the shade tolerance index recently developed by Humbert *et al.* (2006). They provided a light index (or a light preference index) from 1 (very shade tolerant) to 9 (very intolerant) for a large range of species found in Québec. We estimated the light environment using the average light index of all understory species found in each relevé (without the target species) when the number of species appearing in it and in the index was greater than ten. Relevés which did not have more than ten species were not considered.

2.2.2 Statistics

To test our hypotheses, we first have to make the assumption that species follow the realized niche concept (Hutchinson, 1957). This implies that species abundance in a community can be obtained by a Gaussian logistic regression (GLR). The choice of GLR was based on the idea that the response of a species to an environmental gradient can be represented as a smooth and noiseless Gaussian curve (Whittaker *et al.*, 1973). If a species follows this Gaussian ideal then its response could be described by the mean position on the environmental gradient, the standard deviation along the gradient, and by the probability of occurance. It has, however, been suggested that the Gaussian model can have three major limitations with real data (McCune *et al.*, 2002) : (1) some parts of the curve can be outside of the realistic range, (2) the abundance of a species may not be at its maximum potential and the resulting distribution is consequently truncated in some classes, and (3) species can have two or more distinct populations reacting differently to the environmental variables. GLR (Ter Braak and Looman, 1986) was used to estimate both pH and light for species with at least 25 data points (*e.g.* Roy *et al.*, 2000), by fitting the logistic equation with a quadratic function. For each GLR, we determined the maximum of the curve, and one of the distribution coefficients of Pearson (1894), α_4 (also known as the kurtosis), a value obtained from the centred moment of the fourth order.

In order to determine the statistical significance of the relationship, the goodness-of-fit of the model was tested using chi-square statistics (0.10 significance level was used). The resulting quadratic functions with a positive second order coefficient (negative hyperbola) are considered as non significant. After GLR was computed for all species,

the maximum and the kurtosis of all species were evaluated using a scatter-plot to test our hypothesis with two groups : statistically significant species and non-significant species. We applied different models to the scatter-plotted data using general linear regression. These models were linear, logarithmic, second order curve (hyperbola) and Gaussian curve. Model selection was made by analysis of the AIC (Sakamoto *et al.*, 1986), significance of the variables at 0.05 and the r^2. Computations were made using R with the glm function (R Development Core Team, 2005).

2.3 Results and discussion

2.3.1 Gaussian logistic regression

Compilation of the data from the ecological studies provided us with 96 species (33 woody and 63 herbaceous species) with sufficient data for analysis. More than 15 species per relevé were found for each of pH 7.5, 5.5 and 5 (Figure 2.2a). Clearly 40% of the relevés were at pH 4.5 (Figure 2.2b) and all other pH levels were represented by approximately the same number of relevés ($\approx$ 8%). Gaussian logistic regression applied to theses species was significant for 46 species for the pH gradient, 45 species for the light gradient and 29 species for both gradients (See table 2.1 for the preference for the gradient and the kurtosis). Half of the species seem to follow the Gaussian ideal. Moreover, results that could be interpreted as biological inconsistencies were considered to be not significant. For example, the pH preference of 9.92 for *Betula alleghaniensis* or the 14.12 pH value for *Pinus strobus*, as well as some negative values, were all obtained for species that did not have many replicates and therefore were not significant. Similar examples can be provided for the light results.

TAB. 2.1: General results for pH and light (L) gradients obtained with Gaussian logistic regressions. Species are referred to by their scientific names ; Strata refers to the woody (W) and herbaceous(H) stratum ; Pref. refers to the preference ; K. refers to the kurtosis of the curve obtained by Gaussian logistic regression. The column St. indicates significant ; significant models are labelled by * when variables respond significantly at $\alpha = 0.10$.

Species	Strata	Pref. pH	K. pH	St.	Pref. L	K. L	St.
Abies balsamea	W	6.06	3.87	*	4.83	5.71	
Acer pensylvanicum	W	5.59	7.3	*	4.02	2.16	
Acer rubrum	W	3.94	8.93	*	4.49	3	*
Acer saccharum	W	4.63	4.38		6.61	10.98	
Acer spicatum	W	6.48	2.97	*	4.33	3.95	*
Actaea rubra	H	7.19	1.96	*	4.14	2.78	

Species	Strata	Pref. pH	K. pH	St.	Pref. L	K. L	St.
Alnus incana ssp rugosa	W	10.33	1.55		5.38	3.66	*
Amelanchier bartramiana	W	5.79	4.42	*	4.54	2.88	*
Aralia nudicaulis	H	7.53	4.73		2.88	7.03	
Aster puniceus	H	8.17	2.43	*	5.37	3.85	*
Athyrium filix femina	H	7.49	1.86	*	4.19	3.04	*
Betula alleghaniensis	W	9.92	10.97		0.63	6.25	
Betula papyrifera	W	5.16	7.42	*	4.9	2.26	*
Botrychium virginianum	H	6.57	1.56	*			
Carex arctata	H	4.31	2.2		3.88	3.65	
Carex intumescens	H	3.53	7.84		10.94	4.76	
Chimaphila umbellata	H	5.57	5.45	*	4.5	2.72	*
Cinna latifolia	H	5.91	5.21		4.41	2.78	
Circaea alpina	H	8.17	1.68	*	4.57	2.46	*
Claytonia caroliniana	H	5.75	2.46	*			
Clintonia borealis	H	9.09	5.19		3.32	4.68	
Coptis trifolia	H	7.24	5.89		4.21	3.42	*
Cornus alternifolia	W	6.33	3.28	*	3.89	2.66	
Cornus canadensis	W	4.26	5.36		5.07	5.8	*
Cornus sericea ssp sericea	W	7.54	1.71	*	6.32	4.41	*
Corylus cornuta	W	6.16	3.51	*	3.98	4.67	
Cypripedium acaule	H	6.43	2.99		5.67	2.19	
Diervilla lonicera	W	2.33	5.55		5.28	2.92	*
Dryopteris carthusiana	H	4.93	3.67		8.44	3.93	
Epilobium angustifolium	H	5.88	3.84	*			
Equisetum sylvaticum	H	10.25	1.61		4.82	2.9	
Erythronium americanum	H	6.08	2.04	*			
Eurybia macrophylla	H	1.05	2.5		6.02	4.84	*
Fragaria virginiana	H	6.19	2.09	*	7.27	3.53	*
Galium kamtschaticum	H	5.83	2.71	*			
Galium trifolium	H	-0.78	1.67		3.15	2.96	
Gaultheria hispidula	H	5.78	3.39		5.14	3.98	
Gaultheria procumbens	H	7.43	5.02				
Gymnocarpium disjunctum	H	9.18	2	*	10.3	2.64	
Hieracium caespitosum	H	6.4	2.43	*	6.29	4.48	*
Kalmia angustifolia	W	6.13	4.46				
Linnaea borealis	H	7.05	3.74		4.68	2.45	*
Lonicera canadensis	W	5.46	3.42	*	-19.86	6.42	
Lycopodium annotinum	H	4.74	5.57	*	5.11	4.42	*
Lycopodium lucidulum	H	2.66	4.7		5.95	4.96	
Lycopodium obscurum	H	0.78	2.6		7.78	3.41	
Maianthemum canadense	H	1.51	6.21		1.83	5.97	
Maianthemum trifolium	H	5.89	4.24		6.05	3.64	
Medeola virginiana	H	0.05	4.67		24.05	4.72	
Mitella nuda	H	7.69	1.69	*	4.08	2.92	*
Moneses uniflora	H	6.06	4.35	*	4.52	4.42	*
Monotropa uniflora	H	10.54	7.94		6.28	4.88	
Oclemena acuminata	H	7.65	2.61				
Orthilia secunda	H	5.85	4.2	*	4.4	4.19	*
Oryzopsis asperifolia	H	10.59	3.52				
Osmunda cinnamomea	H	6.71	2.13	*	4.64	3.19	*
Osmunda claytoniana	H	4.83	5.05				

Species	Strata	Pref. pH	K. pH	St.	Pref. L	K. L	St.
Oxalis acetosella	H	6.54	4.41		8.05	4.18	
Phegopteris connectilis	H	7.02	3.44		6.91	4.64	
Picea glauca	W	6.7	2.83	*	5.27	6.63	*
Picea mariana	W	4.79	8.93	*	5.23	3.87	*
Pinus strobus	W	14.12	2.39		5.23	2.06	*
Polygonatum pubescens	H	9.66	3.92		6.28	15.59	
Prenanthes altissima	H	7.5	1.54	*	3.96	2.63	
Prenanthes trifoliolata	H	6.84	1.84	*			
Prunus pensylvanica	W	5.66	4.98	*	4.93	2.56	*
Prunus virginiana	W	9.87	2.39		5.4	3.83	*
Pteridium aquilinum	H	-0.4	3.78		5.59	5.52	*
Pteritis pensylvanica	H	7.76	2.96	*	4.5	3.03	*
Pyrola asarifolia	H	6.8	2	*	4.25	2.36	*
Pyrola elliptica	H	6.07	2.4	*	4.09	2.69	
Quercus rubra	W	3.68	6.42		6.23	6.45	
Ribes glandulosum	W	5.85	3.82		4.74	1.98	*
Ribes lacustre	W	7.57	1.76	*	5.11	3.27	*
Ribes triste	W	8.31	1.62	*	4.52	2.08	*
Rubus idaeus	H	7.89	2.01	*	5.49	6.55	*
Rubus pubescens	H	8.03	2.21	*	4.54	3.26	*
Sambucus racemosa ssp pubens	W	11.71	1.96		4.61	2.27	*
Smilacina racemosa	H	3.62	3.77		33.5	11.8	
Solidago macrophylla	H	6.07	2.96	*	4.26	7.61	*
Solidago rugosa	H	6.79	1.86	*			
Sorbus decora	W	6.06	4.06	*	5.01	4.39	*
Streptopus lanceolatus var roseus	H	9.76	4.69		0.48	4.05	
Taxus canadensis	W	4.43	7.16	*	2.12	3.79	
Thalictrum pubescens	H	8.93	1.97	*	5.56	3.13	*
Thuja occidentalis	W	4.7	1.5		4.92	3.13	*
Trientalis borealis	H	4.37	4.83		2.27	5.14	
Trillium cernuum	H	9.15	1.51		4.45	2.63	*
Trillium erectum	H	9.71	6.39		2.8	2.88	
Trillium undulatum	H	6.75	5.87				
Vaccinium angustifolium	W	7.93	3.47		5.57	4.67	*
Vaccinium myrtilloides	W	10.39	2.47		5.86	4.33	*
Viburnum edule	W	6.46	2.37	*	4.54	2.25	*
Viola incognita	H	3.61	3.51		12.47	2.51	
Viola macloskeyi ssp pallens	H	6.3	1.89	*	4.61	3.71	
Viola renifolia	H	3.28	3.51		3.91	2.66	

2.3.2 General patterns

As hypothesized here, if a species response to an environmental variable is Gaussian, values describing the curve should describe the response. Consequently, the maximum of the curve (horizontal asymptote) describes the preference and the kurtosis (α_4) of the curve describes the niche breadth of the species for a given environmental variable.

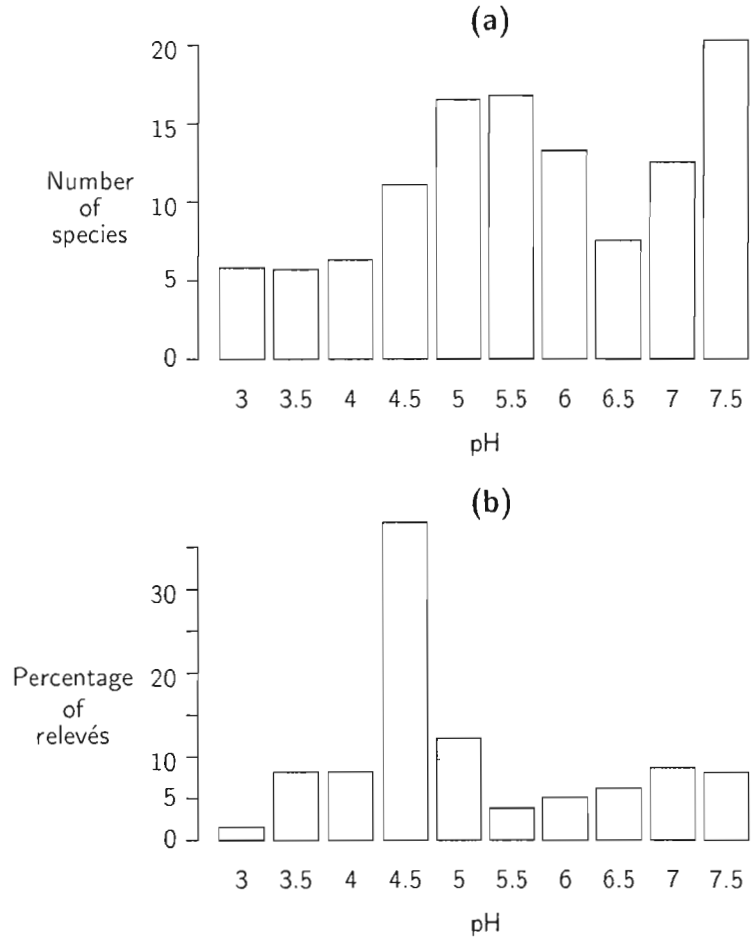

FIG. 2.2: Distribution of species and percentage of relevés along the pH gradient for studies reviewed, with (a) the species richness for each pH levels and (b) the representation of soil pH within all relevés

In accordance with our main hypothesis, we tested whether a pattern exists between (Figure 2.3) : the mean preference for pH and its α_4 ; the mean preference for light and its α_4; the mean preference of one and α_4 of the other gradients; both α_4 and both mean preferences. A negative hyperbolic pattern was found between the mean for preference pH and its α_4 (Figure 2.3 a). A strong orthogonality occurred between the kurtosis of species response to light and the mean preference for light (Figure 2.3 b), pH, α_4 and the mean preference for light (Figure 2.3 d) and the two mean preferences (Figure 2.3 e). No such pattern was found for the other relations tested.

The relationship between niche breadth and pH was tested as described in section

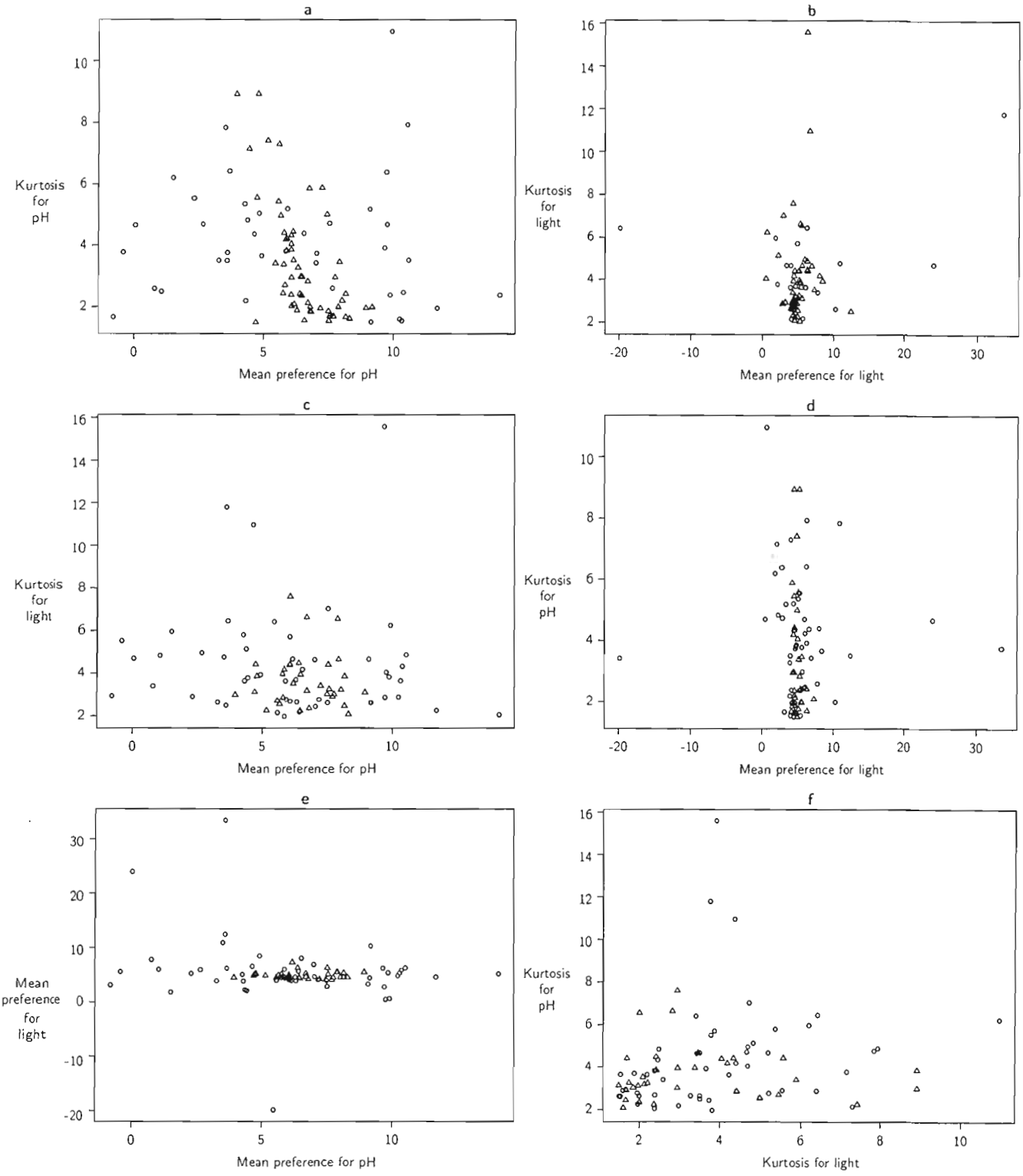

FIG. 2.3: Relationship between the different values derived from the Gaussian logistic regression for pH and light gradients. Circles show non-significant values and triangles show significant values extracted from Gaussian logistic regression for a 0.10 significant level

TAB. 2.2: The regression between the preference and the kurtosis for the pH gradient

Coefficients	Estimate	Std. Error	t value	$Pr(>\mid t \mid)$
Intercept	33.80	3.53	9.572	3.20e-12
X	-8.09	1.07	-7.56	2.03e-09
X^2	0.51	0.08	6.37	1.05e-07
Residual standard error :	0.93	on 43 d.o.f.		
R^2 :	0.78			

2.2.2. Although all models were significant, the hyperbola curve best described the pattern (Figure 2.4 a) with an R^2 of 0.78 (statistics are given in table 2.2). This result supports the specialization hypothesis (Lortie and Aarssen, 1996) and follows our hypothesised pattern (Figure 2.1). This relationship (Figure 4), suggests that the realised niche decreases when the pH becomes more acidic. Our results support the findings of Siccama *et al.* (1970), that soil pH is a strong influencing variable for the distribution of understory forest herbaceous species. Interestingly, this result contradicts the model proposed by Tilman in 2004 (Figure 5d) where the niche breadth increases at the edge of an environmental gradient. He predicted that stochastic competitive assemblies would provide relatively constant niche widths due to species convergence. However, this model seems suitable only for spatially and temporally unstable environmental variables. Moreover, our findings follow the diversity gradient which indicates that competition segregates large niche breadth species or generalists from the other less competitive species found in soil requiring specialization.

At the view of these results, we can asked what might be the mechanisms involved in causing this plasticity ? Although we are not able to completely resolve this question some clues can be identified. As an exemple of possible mechanisms, Van der Krift *et al.* (2001) and Hertenberger *et al.* (2002) have shown that species can improve mineralisation through rhizodeposition and litter production. These mechanisms can be part of the adaptation of a species to specialised conditions, but this strategy of releasing compounds has a high energetic cost. Consequently, theses species may be less competitive in other environments due to the energy that is lost when rhizodeposition is not needed.

Regarding the light gradient, our results indicate a strong orthogonality between the light preference and species niche breadth. Statistically, such orthogonality reflects independence or non-association between variables when the correlation between them

TAB. 2.3: Student's t-test results concerning the slope of the linear regression between broad characteristics of species distribution for light and pH. Null hypothesis tested : β_1 (the slope) is not different from zero. dof refers to the degree of freedom and varies according to the significance of the Gaussian logistic regression (a value of 81 dof corresponds to a test on all results. When the value was 49 or 31, the test was applied only to significant species). The last column gives the result of the test, 1 for yes : $\beta_1 \neq 0$, and 0 for no : $\beta_1 = 0$.

Linear relation tested	β_1	t	dof	$\beta_1 \neq 0$ at 0.05 confidence
Preference for light as f(light kurtosis)	0.60	2.12	43	1
	0.49	1.929	81	0
Preference for light as f(pH kurtosis)	-0.08	-0.832	27	0
	-0.06	1.929	81	0
Preference for light as f(pH preference)	0.05	0.298	27	0
	-0.37	1.929	83	0

is zero (Tabachnick and Fidell, 2000). The significance of this orthogonality was investigated using a Student's t-test on the slope of the linear regression (Table 2.3). Results of the t-test confirms the orthogonality, only the slope between each light characteristic for significant species is different from 0 (Figure 2.4 b). This slope with a value of 0.59 (and a standard error of 0.28 not shown) for this relationship may have little biological significance due to an R^2 near zero. Two explanations can be formulated : (1) calculation of the kurtosis for understory light does not reflect species niche breadth, or (2) understory light is not the environmental factor which drives a broad species distribution of understory plants. Our results tend to refute the first explanation because the kurtosis was found to be a good measure of niche breadth for the pH gradient. The observed orthogonality may also be due to the way we calculated the light environment using the indices from Humbert *et al.* (2006). This index averaging has been widely used and follows the methods and recommendations described by Ellenberg *et al.* (1992). Our study, therefore, suggests that the second explanation is more plausible; light is not a discriminant resource in terms of the broad distribution of understory plant species. Also, most shade-intolerant tree species can be found in shade, at least for a part of their life cycle as reported by Kneeshaw *et al.* (2006).

Finally, the orthogonality between a species' mean preference for light and pH characteristics suggests that soil nutrition is not related to light requirement, also noted by Elemans (2004). As stated before, this result is not surprising since light appears

to be a minor factor explaining the species distribution of the studied understory plant species.

2.4 Conclusion

The careful analysis of species distribution along two broad environmental gradients can lead to determining general patterns in species distribution. In this study, using data dealt with similarly in the literature on the relationships between species abundance and pH and light gradients, we were able to show a strong relationship between the niche breadth and the pH, but we could not find such a relationship with light. Our results also confirm the specialization hypothesis, at least for pH. Species found in more acidic environments have a narrower niche breadth, but the mechanisms underlying this have yet to be elucidated. Understory plant species do not appear to distribute themselves clearly along the light gradient. Athough light has been shown to affect growth and survival, our study shows that light is less constraining than pH. Soil pH is clearly a more complex environmental variable than light and it may call for much more specific physiological adaptations. Also, soil pH is a much more temporally stable environmental variable than light. Gendron *et al.* (2001) have shown that for a given understory microsite, light varies greatly temporally both within a day and over the growing season. Furthermore, light at any point in the understory is likely to change from year to year due to the dynamics of the forest and the recurrent and frequent small-scale disturbances that continuously occur. Although changes in soil pH do occur over time (Bigelow and Canham, 2002), changes are much more gradual and less extreme than for light. Our study further suggests that plant species tend to develop niche specialization only for those environmental factors that are temporally and spatially stable. The stochastic niche theory (Tilman, 2004) makes predictions of interspecific competition for resources, but its predictions seem to work only for non-temporally stable variables, such as light or temperature. The lack of niche breadth of understory plant species in relation to light may help explain why, in some conditions, the neutral theory better explains species distribution in the forest understory than the niche theory (see Chave, 2004, for a review).

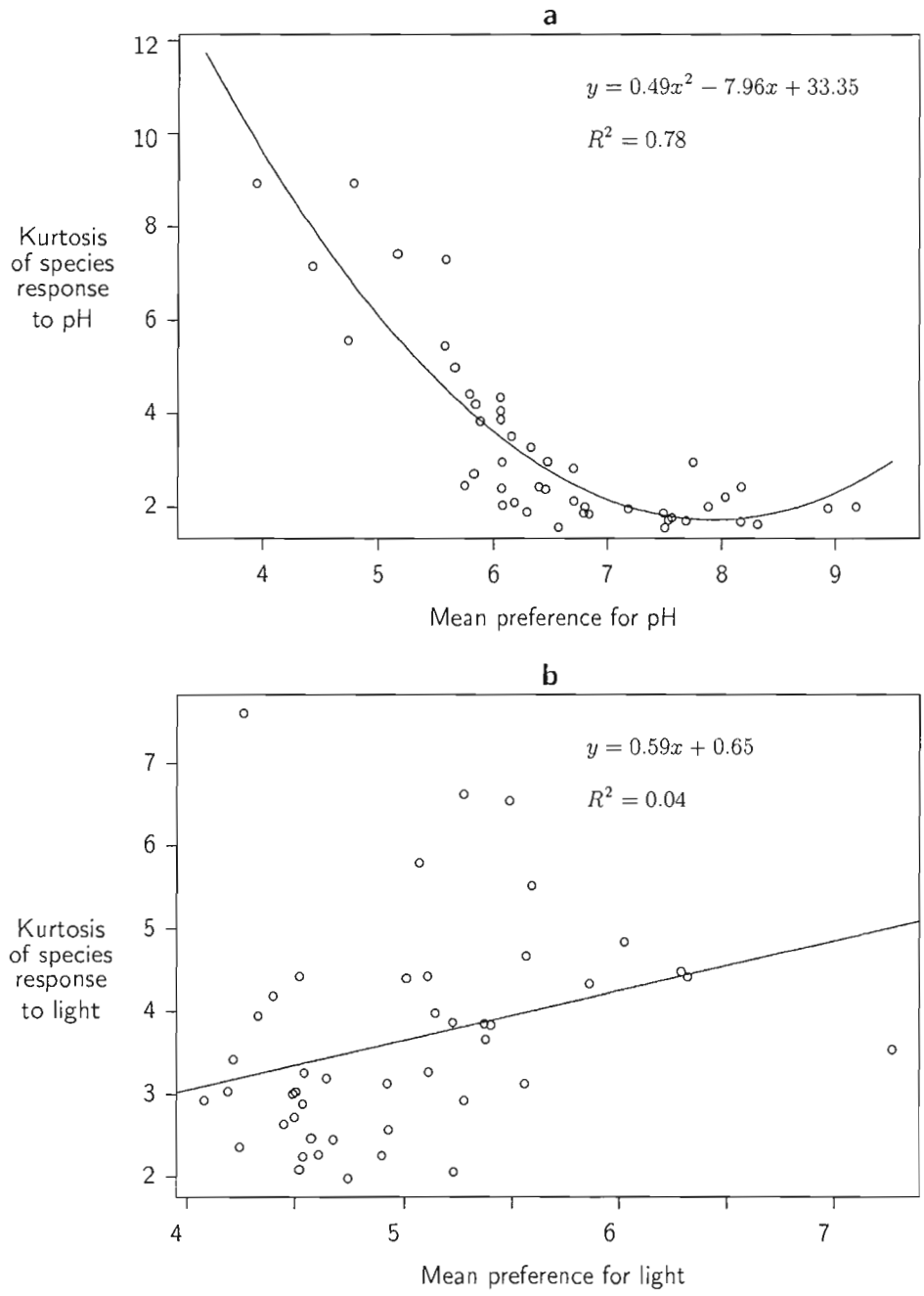

FIG. 2.4: General pattern between the mean preference and the kurtosis of species response for pH (a) and light (b).

BIBLIOGRAPHIE

Agrawal A.A., 2001. Phenotypic plasticity in the interactions and evolution of species. Science 294 : 321–326.

Agrawal A.A., Laforsch C. and Tollrian R., 1999. Transgenerational induction of defenses in animals and plants. Nature 401 : 60–63.

Alpert P. and Simms E.L., 2002. The relative advantages of plasticity and fixity in different environments : when is it good for a plant to adjust ? Evolutionary Ecology 16(3) : 285–297.

Anderson R.C., Loucks O.L. and Swain A.M., 1969. Herbaceous response to canopy cover, light intensity and through fall precipitation in coniferous forests. Ecology 50(2) : 255–263.

Bergeron Y., Bouchard A., Gangloff P. and Camiré C., 1985. La classification écologique des milieux forestiers de la partie ouest des cantons d'Hébécourt et de Roquemaure en Abitibi, Québec. Etudes Ecol. Lab. Ecol. Forest., Univ. Laval Press, Québec, Qc., vol. 9, 169 p. (in French)

Bradshaw A.D., 1965. Evolutionary significance of phenotypic plasticity in plants. Advances in Genetics 13 : 115–155.

Bratton S., 1976. Resource division in an understory herb community : Responses to temporal and micro-topographic gradients. American Naturalist 110 : 233–693.

Braun-Blanquet J., 1964. Pflanzensoziologie, Grundzüge der Vegetationskunde. Springer Verlag, Vienna, 3^{rd} edition, 865 p. (in German)

Brown J.-L., 1981. Les forêts du Témiscamingue, Québec. Ecologie et photointerprétation. Etudes Ecol. Lab. Ecol. Forest., Univ. Laval Press, Québec, Qc., vol. 5, 447 p. (in French)

Bigelow S.W. and Canham C.D., 2002. Community organization of tree species along soil gradients in a north-eastern USA forest. Journal of Ecology 90 : 188–200.

Chase J.M. and Leibold M.A., 2003. Ecological niches. University of Chicago Press, Chicago, IL., 221 p.

Chave J., 2004. Neutral theory and community ecology. Ecology Letters 7 : 241–253.

Dong M., During H.J. and Werger M.J.A., 1996. Morphological responses to nutrient availability in four clonal herbs. Vegetatio 123 : 183–192.

Elemans M., 2004. Light, nutrients and the growth of herbaceous forest species. Acta Oecologica 26(3) : 197–202.

Ellenberg H., Weber H.E., Düll, R., Wirth V., Werner W. and Paulissen D., 1992. Zeigerwerte von Pflanzen in Mitteleuropa. Scripta Geobotanica 18 : 1–258. (in German)

Emery R.N.J., Chinnappa C.C. and Chmielewski J.G., 1994. Specialization, plant strategies, and phenotypic plasticity in populations of Stellaria longipes along an elevational gradient. International Journal of Plant Sciences 155 : 203–219.

Gendron F., Messier C. and Comeau P.G., 2001.Temporal variations in the understorey photosynthetic photon flux density of a deciduous stand : the effects of canopy development, solar elevation, and sky conditions. Agricultural and Forest Meteorology 106 : 23–40.

Givnish T.J., 2002 Ecological constraints on the evolution of plasticity in plants. Evolutionary Ecology 16(3) : 213–242.

Grandtner M.M., 1969. La végétation forestière du Québec méridional. Univ. Laval Press, Québec, Qc., 2^d edition, 216 p. (in French)

Hertenberger G., Zampach P. and Bachmann G., 2002. Plant species affect the concentration of free sugars and free amino acids in different types of soil. Journal of Plant Nutrition and Soil Science 165 : 557–565.

Humbert L., Gagnon D., Kneeshaw D. and Messier C., 2006. A shade tolerance index for common understory species of northeastern North America. Ecological Indicators. (in press)

Hutchings M.J. and de Kroon H., 1994. Foraging in plants : the role of morphological plasticity in resource acquisition. Advances in Ecological Research 25 : 159–238.

Hutchinson G.E., 1957. Concluding remarks. – Cold Spring Harbor Symposia on Quantitative Biology 22 : 415–427.

Karban R., Baldwin I.T., Baxter K.J., Laue G. and Felton G.W., 2000. Communication between plants : induced resistance in wild tobacco plants following clipping of neighboring sagebrush. Oecologia 125 : 66–71.

Kneeshaw D.D. , Kobe R.K., Coates K.D. and Messier C. Sapling size influences shade tolerance ranking among southern boreal tree species. Journal of Ecology 94 : 471–480.

Lortie C.J. and Aarssen L.W., 1996. The specialization hypothesis for phenotypic plasticity in plants. International Journal of Plant Sciences 157(4) : 484–487.

Majcen Z., 1981. Les forêts du parc national Forillon, Gaspésie, Québec : étude phytosociologique. Etudes Ecol. Lab. Ecol. Forest., Univ. Laval Press, Québec, Qc., vol. 4, 158 p. (in French)

McCune B., Grace J. B. and Urban D. L., 2002. Analysis of ecological comunities. MjM Software Design, Glenedon Beach, OR., 304 p.

Pearson K., 1894. Contributions to the mathematical theory of evolution. Philosophical Transactions of the Royal Society A 185 : 71–110.

R Development Core Team, 2005. R : A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. (http//www.R–project.org)

Roy D.B., Hill M.O., Rothery P. and Bunce R.G.H., 2000. Ecological indicator values of British species : an application of Gaussian logistic regression. Annales Botanici Fennici 37 : 219–226.

Schlichting C.D. and Pigliucci M., 1998. Phenotypic evolution : a reaction norm perspective. Sinauer Press, Sunderland, MA, 340 p.

Sakamoto Y., Ishiguro M. and Kitagawa G., 1986. Akaike Information Criterion Statistics. Springer, New York, LLC, 320 p.

Siccama T.G., Bormann F.H. and Likens G.E., 1970. The Hubbard Brook ecosystem study : productivity, nutrients, and phytosociology of the herbaceous layer. Ecological Monographs 40(4) : 389–402.

Tabachnick B.G. and Fidell L.S., 2000. Using Multivariate Statistics. Allyn and Bacon, Boston, 4^{th} edition, 932 p.

Ter Braak C. J. and Looman C. W. N., 1986. Weighted averaging, logistic regression and the Gaussian response model. Vegetatio 65 : 3–11.

Tilman D., 2004. Inaugural Article : Niche tradeoffs, neutrality, and community structure : A stochastic theory of resource competition, invasion, and community assembly. Proceedings of the National Academy of Sciences of the United States of America 101 : 10854–10861.

Valladares F., Wright J.S., Lasso E., Kitajima K. and Pearcy R.W., 2000. Plastic phenotypic response to light of 16 congeneric shrubs from a Panamanian rainforest. Ecology 81(7) : 1925–1936.

Van Assche F. and Clijsters H., 1990. Effects of metals on enzyme activity in plants. Plant Cell Environment 13 : 195–206.

Van Dam N.M. and Baldwin I.T., 2001. Competition mediates costs of jasmonate-induced defences, nitrogen acquisition and transgenerational plasticity in *Nicotiana attenuata*. Functional Ecology 15 : 406–415.

Van der Krift T., Kuikman P., Moller F. and Berendse F., 2001. Plant species and nutritional-mediated control over rhizodeposition and root decomposition. Plant and Soil 228(2) : 191–200.

Whittaker R. H., Levin S. A. and Root, R.B., 1973. Niche, habitat, and ecotype. American Naturalist 107 : 321–338.

CONCLUSION

L'objectif de ce mémoire était de mieux caractériser deux indicateurs écologiques très utilisés pour les plantes forestières, soit la tolérance à l'ombre et au pH des espèces de sous-bois, et cela dans le but de fournir des outils d'aménagement et de conservation.

L'indice de tolérance à l'ombre pour les espèces de sous-bois nord-américaines a été construit afin qu'il soit robuste et largement utilisable. Il a permis d'établir une cote de 1 à 9 pour 347 espèces. Parmi ces espèces on compte 71 ligneuses, 185 herbacées et 91 bryophytes et lichens. La corrélation entre les données européennes et celles obtenues pour l'Amérique du Nord est très bonne et met en évidence le maintien des caractéristiques écologiques entre les deux continents. Cet indice est surtout théorique, car pour ce qui est de la tolérance à l'ombre observée en forêt, elle a été calculée (comme pour le pH) par des régressions logistiques gaussiennes pour seulement 51 espèces. Pour le pH, seulement 56 espèces ont été indicées par régression logistique gaussiennes. L'approche par indicateurs mise en place ici est très prometteuse, car l'existence d'un assemblage végétal est le fruit d'un équilibre fin entre espèces. L'existence simultanée d'espèces est due aux caractéristiques de l'environnement et aux mécanismes de compétition. Cette approche doit permettre aux aménagistes forestiers d'avoir des outils qui réduisent la complexité et les mesures complexes en ayant un faible coût, tout en permetant de représenter convenablement la complexité de l'écosystème (Müller and Lenz, 2006).

Les régressions logistiques nous ont également permis de calculer le kurtosis des distributions des espèces selon les conditions de pH et de lumière. Cette valeur est intéressante puisqu'elle nous permet de mieux déterminer l'amplitude écologique de ces espèces par rapport à nos deux variables écologiques. Cette amplitude écologique pourrait être définie comme un indice de plasticité génotypique de l'espèce. Un tel indice nous permet de savoir si telle ou telle espèce est un bon indicateur des conditions écologiques définies. En effet, une espèce très plastique fournira moins d'informations sur l'environnement qui l'entoure qu'une espèce faiblement plastique ne pouvant survivre que dans des conditions écologiques bien précises. La relation entre le kurtosis et le pH est très forte. Cela va dans le sens de l'hypothèse de la spécialisation, à savoir que les espèces de milieu très acide se sont adaptées à ces conditions écologiques particulières et de ce fait elles auraient perdu leur capacité à endurer des pH plus élevés. Pour la lumière, cette même relation est orthogonale. En termes biologiques, cela veut dire que les espèces d'ombre sont aussi capables d'évoluer dans des milieux plus lumineux et vice et versa. La lumière serait donc une condition écologique moins discriminante que

le pH. Ce résultat a priori surprenant, peut cependant s'expliquer. Une adaptation au pH demande des changements de fonctionnement au niveau cellulaire assez importants qui sont surtout reliés à des problèmes osmotiques, de charges électriques ainsi qu'aux pertes de solubilités de certains ions essentiels. Par contre, une adaptation à la lumière demande des changements aux niveaux des photosystèmes moins importants et surtout cela peut se faire rapidement comme on le voit lors du phénomène d'induction chez les plantes. Il y a certainement des plantes qui sont de véritables spécialistes de faible ou pleine lumière, mais globalement la tolérance à l'ombre serait le fait d'une moins grande compétition de certaines espèces lorsque la lumière est faible plutôt qu'une adaptation bien précise à des conditions lumineuses particulières. Ceci a été montré récemment dans plusieurs revues de littérature (*e.g.* Messier *et al.*, 1999). On définit souvent la tolérance à l'ombre comme étant la capacité d'une espèce à tolérer l'ombre, ce mot tolérer va bien dans le sens d'une faible compétitivité. Enfin, les nombreuses études contradictoires sur la tolérance à l'ombre appuient également cette redéfinition.

Pour conclure, les connaissances apportées par ce mémoire devraient permettre de mieux comprendre et suivre la dynamique de la végétation de sous-bois dans nos écosystèmes forestiers.

BIBLIOGRAPHIE

Anderson R.C., Loucks O.L. and Swain A.M., 1969. Herbaceous response to canopy cover, light intensity and through fall precipitation in coniferous forests. Ecology 50(2) : 255–263.

Baker F. S., 1949. A revised tolerance table. J. For. 47 : 179–181.

Bratton S., 1976. Ressource division in an understory herb community : Responses to temporal and micro-topographic gradients. American Naturalist 110 : 233–693.

Braun-Blanquet J., 1964. Pflanzensoziologie, Grundzüge der Vegetationskunde. Springer Verlag, Vienna, 3^{rd} edition, 865 p. (in German)

Chapin F.S. III, 1980. The mineral nutrition of wild plants. Annual Review of Ecology and Systematics 11 : 233–260.

Duchaufour P., 1982. Pedology : Pedogenesis and Classification. George Allen and Unwin, London, 442 p.

Dupouey J.L., Dambrine E., Laffite J.D. and Moares C., 2002. Irreversible impact of past land use on forest soils and biodiversity. Ecology 83(11) : 2978–2984.

Ellenberg H., Weber H.E., Düll R., Wirth V., Werner W., Paulissen D., 1992. Zeigerwerte von Pflanzen in Mitteleuropa. Scripta Geobotanica 18 : 1-258. (in German)

Gilliam F.S., 1988. Interactions of Fire with Nutrients in the Herbaceous Layer of a Nutrient- Poor Coastal Plain Forest. Bulletin of the Torrey Botanical Club 115(4) : 265–271.

Gilliam F.S. and Turrill N.L., 1993. Herbaceous Layer Cover and Biomass in a Young Versus a Mature Stand of a Central Appalachian Hardwood Forest. Bulletin of the Torrey Botanical Club 120(4) : 445–450.

Hutchinson B.A., Matt D.R., 1977. The annual cycle of solar radiation in a deciduous forest. Agric. Meteorol. 18 : 255–265.

Ling K.A., 2003. Using environmental and growth characteristics of plants to detect long-term changes in response to atmospheric pollution : some examples from British beechwoods. The Science of The Total Environment 310(1-3) : 203–210.

Lortie C.J. and Aarssen L.W., 1996. The specialization hypothesis for phenotypic plasticity in plants. International Journal of Plant Sciences 157(4) : 484–487.

Messier C., Doucet R., Ruel J.C., Claveau Y., Kelly C. and Lechowicz M.J., 1999. Functional ecology of advance regeneration in relation to light in boreal forests. Canadian Journal of Forest Research 29 : 812–823.

Müller F. and Lenz R., 2006. Ecological Indicators : Theoretical fundamentals of consistent applications in environmental management. Ecological indicators 6(1) : 1–5.

Peterson D.L. and Rolfe G.L., 1981. Nutrient dynamics of herbaceous vegetation in upland and flood plain forest communities. American Midland Naturalist 197 : 325–339.

Schuck A., Parviainen J. and Bücking W., 1994. EFI Working Papers No 3. A Review of Approaches to Forestry Research on Structure, Succession and Biodiversity of Undisturbed and Semi-natural Forests and Woodlands in Europe. ISBN 952-9844-02-6. 62 p.

Siccama T.G., Bormann F.H. and Likens G.E., 1970. The Hubbard Brook ecosystem study : productivity, nutrients, and phytosociology of the herbaceous layer. Ecological Monographs 40(4) : 389–402.

Shirley H.L., 1943. Is tolerance the capacity to endure shade? Journal of Forestry 41 : 339–345.

Soltner D., 2000. Phytotechnie générale : les bases de la production végétales. Tome 1 : le sol et son amélioration. Sciences et techniques agricoles, 22^{ieme} édition, 467 p.

Wilson S.M., Pyatt D.G., Malcolm D.C., Connolly T., 2001. The use of ground vegetation and humus type as indicators of soil nutrient regime for an ecological site classification of British forests. Forest Ecology and Management 140(2-3) : 101–116.